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THE COLORS OF NORTHERN GAMOPETALOUS FLOWERS.[1]

JOHN H. LOVELL.

THE Gamopetalæ are characterized by the more or less united petals. This series is not derived from the Choripetalæ, but represents an independent though parallel line of development. The union of the petals has not been induced by insects, and "is not," says Gœbel, "the result of a cohesion of originally free parts, but is due to the excessive growth of the zone of the floral axis in which the rudiments of the petals are inserted." Much uncertainty prevails as to the phylogeny of the gamopetalous series, which can only be settled by further investigation. There are two points of culmination. By common consent the Compositæ are placed at the head of this series and of the plant kingdom. In this family it is the community of flowers rather than the individual flower that is of chief importance. A secondary culmination occurs in the Labiatæ and Scrophular-

[1] The Colors of Northern Monocotyledonous Flowers, *Amer. Nat.*, vol. xxxiii, p. 493; The Colors of Northern Apetalous Flowers, *Amer. Nat.*, vol. xxxv, p. 197; The Colors of Northern Polypetalous Flowers, *Amer. Nat.*, vol. xxxvi, p. 203.

iaceæ, families in which the flowers are zygomorphous and often of large size. It has been suggested that these two divisions represent two distinct lines of development and are of very different origin. The Compositæ are derived through the Rubiaceæ and Caprifoliaceæ from the Umbelliferæ, while the aroids are assigned as the remote ancestors of the labiate forms. It seems better, however, to regard the series as homogeneous. The gamopetalous families probably had a common starting point and are derived from a group of primitive forms allied to the progenitors of the Choripetalæ, but a later offshoot, and still retaining affinities with the monocotyledons. The flowers are characterized by definiteness in the number of parts and by their frequent cohesion, characters, says Engler, which must have become fixed at a very early period in their history. The Gamopetalæ are of later occurrence in the fossil state than the Choripetalæ.

The first of the gamopetalous orders, the Ericales, which includes six families, is the most primitive in structure. The flowers have the corolla lobed or pointed, or the petals may be entirely distinct; the ovary is superior except in the Vacciniaceæ; there are two typical staminal whorls, and the carpels equal the petals in number. In the genera Clethra and Pyrola the petals are but slightly, or not at all united, and in Monotropa and Ledum are regularly separate. Of the 81 flowers belonging to these six families 47 are white and 24 are red; while only 1 is yellow, 6 purple, and 3 green.

The Pyrolaceæ are low perennials with clustered evergreen leaves, growing in woodlands and swamps. The flowers are racemose and 7 of the species are white, 2 red, 1 purple and 1 green. They vary but little in size. Several of the white flowered species of Pyrola are tinged with green, while in Moneses and Chimaphila the white flowers are often pinkish. The purple *Pyrola uliginosa* is a bog plant. The flowers of this family are visited by bees, flies and beetles. The primitive color was doubtless greenish-white, which has varied into pink and purple. Flowers of different sizes have been observed on *P. minor*.

The Monotropaceæ are saprophytes without chlorophyll, and

with the leaves reduced to bracts. The plants which live in rich woods are white or colored with anthocyan. *Monotropa uniflora* (Indian pipe or ghost-flower) is usually pure white, and stands out in strong contrast with the dark brown soil of its woodland home. Occasionally the whole plant is pink or red. Specimens in drying turn black. *M. hypopitys* has the entire plant pale yellow, with yellowish or pink flowers. On the island of Wollin Knuth saw a bumblebee sucking the flowers. The plant of Monotropsis is pale pinkish brown with fragrant pink flowers.

The flowers of the Ericaceæ are produced in great profusion, and often display bright masses of color, which are visible at a long distance. This family reaches its highest development in the temperate zones, the structure and form of the plants enabling them to endure the severities of alpine summits. The heaths proper are most abundant at the Cape of Good Hope, where more than 400 species have been described. Of the 38 northern species 22 are white, 1 yellow, 10 red, and 5 purple.

Some of the handsomest of the wild flowers belong to the genus Azalea. Of the five northern species two are white, one orange and two rose color, and all have large flowers with slender tubes. *A. lutea* (*A. calendulacea*) in spring is covered with orange flowers which turn to flame color. In the Alps on a hot June day the hillocks projecting from the surrounding snow are densely carpeted with the crimson flowers of the smaller and more primitive *A. procumbens* over which flit numerous bees and butterflies. Florists offer hybrids of *A. pontica* from Asia Minor, which display a great range of yellow and red coloring. Closely allied to the Azaleas and equally beautiful are the Rhododendrons. The flowers are red or purple, or in *R. maximum* rose or sometimes white spotted with orange, and are fertilized by bumblebees. *Rhododendron maximum* and *Kalmia latifolia* have been called the two handsomest North American shrubs. Bigelow remarks in his *Medical Botany* that "these shrubs, in luxuriant size and vigor, are seen to cover tracts of great extent, at one season presenting an unbroken landscape of gorgeous flowers." Asa Gray in one of his letters speaking of the glorious view from Roan Mountain, North Carolina, writes, "The valleys and mountains all around, covered with rich forest,

are adorned with *Rhododendron maximum* and *Kalmia latifolia* in immense abundance and profuse blossoming, of every hue from deep rose to white, and here and there among other shrubs *Azalea calendulacea*, of every hue from light yellow to deepest flame color." [1] The flowers of Kalmia are red or red purple and are pollinated by bees. In northern New England the commonest species of Kalmia is *K. angustifolia*, which produces its crimson flowers in late spring. The central flowers of the corymb are smaller and imperfectly developed; the corolla is white and without pouches, while the stamens stand erect and are not exceeded in length by the pistil. Most of the northern genera of the Ericaceæ, however, are shrubby plants with small, white, racemose or clustered, drooping flowers attractive to the honeybee and bumblebees. Such are Andromeda, Leucothoë, and *Gaultheria procumbens*, or the checkerberry. The flowers of this last species are partially concealed beneath the leaves and in the grass and moss, amid which the plant grows. Yet I have found the honeybee and three species of bumblebees very frequent visitors. The aromatic scented flowers are white with reddish calyx and peduncles. It would be difficult to find greater extremes in conspicuousness than is presented by the magnificent color masses of Rhododendron and Kalmia, and the small concealed flowers of Gaultheria, yet these latter do not want for pollinators. None of the true heaths (Erica) are endemic in America, but two species (*E. cinerea* and *E. tetralix*, adventitious from Europe) occur in small patches on the Island of Nantucket. *E. carnea* unlike most red flowers of this family is adapted to butterflies. Both the petals and sepals are pink or crimson, and the peduncles are still more intensely colored. The inverted flowers were doubtless first adapted to bees, as is usually the case with campanulate flowers in this position. The entrance to the corolla has now become so narrowed that only the slender proboscis of the butterfly is admitted. Müller saw a bumblebee in vain striving to suck the honey. In the Alps he found it frequently visited by *Vanessa cardui*.

Of the Vacciniaceæ, or huckleberry family, 10 species are

[1] *Letters of Asa Gray*, vol. ii, p. 692.

white, 11 red, and 2 green. The primitive color of the corolla seems to have been green, as it is still greenish, greenish-white, greenish-pink, or yellowish-green in the genus Vaccinium. The flowers are bell-shaped and the pollinators are bees. *V. pennsylvanicum* (the common blueberry) is white often tinged with red on the side exposed to direct sunlight. At the time of blooming in spring the leaves are reddish, and patches of these bushes on a hillside are visible at a long distance. The flowers of *Gaylussacia resinosa*, or the huckleberry, are red, and the entire plant exhibits a marked tendency to develop red coloration. The floral bracts and stems are reddish, and the leaves when stung by a gall-fly turn a deep red, while the brilliant crimson of the foliage in autumn is unsurpassed. The nodding flowers are visited, according to my observations, by nine species of bees besides several butterflies. If the entrance to the corolla, which is already quite small, should be further narrowed to the exclusion of bees, as has been described in *Erica carnea*, this species would become also adapted to butterflies. It might then readily be assumed that the red coloration had been produced in response to the visits of these insects, whereas it has arisen very early in the history of this flower independently of any supposed preference for this color which butterflies may possess. This the writer believes to have actually happened in the case of not a few red butterfly flowers. Conclusions as to the influence of insects in developing particular colors, it is evident, must be made with great caution. No other gamopetalous families contain so many red flowers as the Ericaceæ and Vacciniaceæ. In the development of red and the exclusion of blue coloring they resemble the Rosaceæ. But in fruit blue and blue black are in the Vacciniaceæ of common occurrence.

In the Primulales there are also two staminal whorls, and distinct petals still occur. The Primulaceæ contain 4 white, 11 yellow, and 7 red flowers. Trientalis, Lysimachia, Steironema, and Anagallis are pollen flowers and contain no nectar. The corolla is small and rotate. The white *Trientalis americana*, (star-flower) grows in damp woodlands, and is rarely visited by insects. *Anagallis arvensis*, or poor-man's weather-glass, has scarlet flowers, which are sometimes white, and in the variety

cærulea are blue. The closing of the flower in the afternoon effects fertilization in the absence of insects. The species of Lysimachia and Steironema are yellow sometimes with a red center, or dark spotted in *Lysimachia quadrifolia* and *L. terrestris*. Of *L. vulgaris* there have been described three forms. The smallest, which grows in the shade, has light yellow flowers with greenish yellow filaments and is self-fertilized. The most conspicuous and largest form grows in sunny localities, has dark yellow petals with a red center and is rarely self-fertilized. The third form is an intermediate one. The flowers of Lysimachia are largely fertilized by bees of the genus Macropis. These pollen flowers, which attract few visits, display white, yellow, red, scarlet and blue colors, and the evidence is wholly insufficient to prove that the coloring has been determined by the selective agency of insects.

The species of Primula, well-known for the laborious investigations of Darwin, are largely dimorphous. The corolla is tubular and the honey is deeply concealed. The flowers are yellow and red. Bumblebees are frequent visitors to the yellow-flowered forms, and Müller found six red-flowered species in the Alps fertilized by butterflies. On *P. farinosa*, which is red with a yellow eye, he collected forty-eight species of Lepidoptera. In Glaux the corolla is wanting and the calyx is pink and petal-like. Sometimes the corolla is duplicated, as in the "hose in hose" flowers of *Primula acaulis*.

The Ebenales contain four families, the Sapotaceæ, Ebenaceæ, Symplocaceæ, and Styraceæ. There are but eight species in the Northern States, two with yellow and six with white flowers. In tropical regions these families are represented by a large number of trees and shrubs of which the most important is the ebony-tree, valued for its black heart wood.

The characters of the Gentianales and Polemoniales are so similar that the two orders cannot be readily distinguished. They differ from the preceding families, which are more closely allied to the Choripetalæ, in having but a single whorl of alternate stamens, and in the smaller number of carpels. Up to this point white and red colors have been most common in the Gamopetalous series, but these two orders are remarkable for containing a large number of purple and blue flowers.

The Gentianales include six families. The olive family, or Oleaceæ, contain two white, one purple and seven green flowers. The green flowers belong to Fraxinus (ash) and are the result of retrogression, as a part of the species have lost both calyx and corolla and are wind-fertilized, while others still retain the perianth. The common lilac (*Syringa vulgaris*) exhibits a great variety of beautiful shades including white, red, purple and blue. Showy yellow flowers occur in Forsythia.

The Loganiaceæ represent the stem-form of the order Gentianales. The presence of stipules distinguishes it from all of the other families of this order. The genera are synthetic in character and exhibit affinities in many different directions. Here are found the ancestral types of the Gentianaceæ, Apocynaceæ and Asclepiadaceæ, as well as of the Scrophulariaceæ and of the Rubiaceæ. The family is abundant in tropical regions but in the Northern States is represented by only four species; one of which is yellow, two white and one red. Our species are related most closely to the Rubiaceæ. The bird flower *Spigelia marilandica* (Maryland pinkroot) is scarlet outside, and yellow within, with a corolla one and one half inches in length, resembling in its coloring *Lonicera sempervirens*.

The Gentianaceæ are the first of the Gamopetalous families in which blue flowers are common. There are 7 white, 1 yellow, 10 red, 4 purple, and 16 blue flowers. The gentians form the most important genus. These plants many of which are characterized by a brilliant blue color are widely distributed in temperate regions, and are very abundant at alpine elevations extending upward to altitudes of over 15,000 feet. The genus contains white, yellow, red, purple and blue flowers. In the mountains of Switzerland the traveller is delighted by the vivid masses of blue coloring displayed by the gentians. Red-flowered species occur in the Andes. Müller regards *Gentiana lutea* as representing the primitive form of this genus. The rotate flowers are yellow with slender pointed petals, which are but slightly united. The honey is fully exposed to beetles and flies as well as to bees, but so few are the visitors that the plant is unable to dispense with spontaneous self-fertilization. The blue bell-shaped flowers have been evolved by bumblebees. The transi-

tion from yellow to blue is shown in *G. purpurea*, which is yellow inside and blue outside. A number of species by the lengthening and narrowing of the corolla have become adapted to Lepidoptera alone, or to bumblebees and Lepidoptera, but the blue color it is noteworthy has been retained. In the genus Sabbatia the handsome flowers are wheel-shaped, and the coloration seems to have changed from yellowish to white or pink, or pink-purple. *S. lanceolata* and *S. paniculata* are white turning yellowish in fading; and *S. augustifolia* and *S. campanulata* are pink with a yellowish eye. Several of the rose-colored species are sometimes white. In Erythraea the slender funnel-form flowers are as the name of the genus denotes usually red. In *Frasera carolinensis* the rotate corolla is light greenish yellow with brown purple dots. Bartonia which grows in swamps and meadows shows evidences of retrogression in the thread-like stems and awl-shaped leaves. The flowers are small and white or yellowish.

The Menyanthaceæ are marsh or aquatic plants, which in our species have yellow or white flowers. The flowers of Limnanthemum (floating-heart) are short-lived. As the petals wither they become pulpy and exude a thin layer of liquid which is attractive to flies. A similar change occurs in Tradescantia.

The Apocynaceæ are confined chiefly to tropical regions. There are only seven species in the northern states but they exhibit a wide range of color, two are white, one yellow, one red, one purple and two are blue. The dogbanes (Apocynum) have small, bell-shaped, white, or pink flowers in cymes. The pinkish flowers of *A. androsæmifolium* are attractive to butterflies. The white species are visited by numerous bees. *Vinca minor*, or the myrtle, is blue, while *V. rosea* from the West Indies is rose or white. Both species are fertilized by bees. The Oleander (Nerium) cultivated from the Levant has large, scentless, showy rose-colored flowers that are fertilized by the hawkmoth Sphinx nerii. The caterpillar of this moth lives exclusively upon the leaves of the oleander. The species of this family in the north are too few to afford much information as to the relations of insects to their coloring.

Like the preceding family the Asclepiadaceæ are most abundant in the tropics. There are 11 white, 3 yellow, 5 red, 13

purple and 7 green flowers. The inflorescence is in umbels. Pollenization in the genus Asclepias is affected in a curious and remarkable manner, analogous in many respects to that of the Orhidaceæ. The pollen coheres in waxy masses called pollinia, which by means of an ingenious clip mechanism are clamped to the legs or antennæ of insects, and are thus transferred from one flower to another. When the pollinia come in contact with the stigma they adhere very firmly, and the insects obtain their freedom by snapping the connecting bands. Conspicuousness is gained by two whorls of petaloid bodies, the corolla and the corona. The corona is composed of five hood-shaped appendages bearing horn-like processes, within which the scented honey is plentifully secreted. The color of the corona is usually the same as that of the corolla, white, orange-red, or purple, though it is frequently of a different shade. But sometimes the flowers are distinctly bicolored; in *A. quadrifolia* the petals are pink and the corona is white, while in *A. lanceolata* the corolla is red and the corona orange. The visitors are Hymenoptera, butterflies and flies. Of the 22 northern species, 2 are greenish, 6 white, 3 yellow or orange, 4 red and 7 purple. The white and greenish-white flowers are the smallest. The two species of Asclepiodora have the corolla greenish and the hoods purplish. In Acerates, or green milk weed, the corolla is greenish and the hoods white, yellow, or purplish. In Vincetoxicum the corona is reduced to an annular ring adnate to the corolla, and the brown or red purple flowers possess a putrid odor attractive to carrion flies. The Asclepiadaceæ is one of the five Gamopetalous families, which contain seven or more greenish flowers. The prevalence of greenish and white flowers and the absence of blue would indicate that the coloring was but little developed in this family. The corona is perhaps analogous in its origin to the ligule of grasses.

The fifth gamopetalous order the Polemoniales, or Tubifloræ, is the largest and most difficult of this series. The families differ but little from each other, and are closely allied to the preceding order. About 900 species belong to the Convolvulaceæ, or morning-glory family, but they are confined chiefly to the tropics. In the Northern States this family contains 7 white,

1 yellow, 7 red and 3 blue flowers. The corolla is campanulate or funnelform. In Ipomœa and Convolvulus many of the flowers are bicolored, or tricolored. *Ipomœa purpurea* is purple, pink, variegated, or white, and a variety in my garden produced a purple flower striped with red, the whole flower fading to red. Both red and purple flowers may occur on the same plant. *I. versicolor* cultivated from Mexico has small, reddish flowers, which change to orange and yellow. *Convolvulus tricolor* has a blue corolla with a whitish throat and a yellow tube. The two species of Quamoclit have scarlet, salverform corollas adapted to humming-birds. The genus Cuscuta is a group of yellow, or orange-colored, parasitic plants destitute of chorophyll, and of world-wide distribution. The flowers are white or tinged with rose. In Maine I have found that the visitors were small bees.

The Polemoniaceæ, or phlox family, are most abundant in the Western States. In the Eastern States there are 7 white, 10 red, 3 purple, and 8 blue flowers. The corolla of Phlox is salverform, and several of the red species have been observed to be fertilized by butterflies. *Phlox paniculata* and *P. drummondii* are favorites in cultivation for the brilliant effects they produce when massed. They have yielded innumerable shades and combinations of white, yellow, red and purple. A large number of the varieties are bicolored, in which the center may be white, red, purple, or even blue. A curious color variation of a perennial phlox of the variety Monsieur Maille is given in the *American Garden* for January, 1890. "In the morning the flowers were of a clear blue, remaining of this color until nearly noon, when they gradually changed to a delicate pink and by evening were a beautiful deep rose. This was repeated every day while the plant was in bloom." Many handsome red and blue flowers occur in the genus Gilia; in *G. tricolor* the lobes of the corolla are purple or white, and the throat brown purple, with a yellow tube. The genus Polemonium possesses pure blue flowers. In *Cobœa scandens* from Mexico the flowers are at first green changing to purple. Yellow is not common in this family. In the Polemoniaceæ, as in the Convolvulaceæ, the flowers are remarkable for the variety of their colors, for the number of combinations of two or more colors in a single flower, and for

the changes of color in individual flowers. These color relations will be again referred to under the Boraginaceæ.

Of the Hydrophyllaceæ 8 species are white and 10 blue. Frequently these latter species revert to white. They are mostly woodland flowers where blue contrasts with the yellowish or brown background. This is a small family intermediate between the preceding family and the Boraginaceæ.

The coloration of few families is so interesting as that of the Boraginaceæ, since the individual flowers often undergo several changes of color, and "seem to recapitulate to us the evolution of their colors." There are some 1500 widely distributed species. The inflorescence is in one-sided scorpioid spikes, racemes, or cymes. The flowers are small and regular, except in Echium, but the corolla varies much in length. In Myosotis and Asperugo the tube is short, and there is a great variety of visitors; while in Borago and Symphytum the flowors are inverted and the honey is accessible only to long-tongued bees. There are 6 yellow, 19 white, 1 purple and 17 blue flowers. *Heliotropum polyphyllum* is white but in variety *leavenworthii* of Florida bright yellow, and in *H. curassavicum* (seaside heliotrope) the corolla is white with a yellow eye, changing to blue. Most of the species are, however, white or blue. The common heliotrope from Peru (*H. peruvianum*) has the tube white with the lobes purple, which in fading grow whitish. In this genus yellow and white appear more primitive than purple or blue. Echinospernum has small bell-shaped flowers, which are visited by flies, bees and moths. *E. lappula* in the bud is white, red before expanding, and afterwards bright blue. The coloration of Myosotis, one of the simpler genera, is remarkably variable. *M. palustris* and *M. laxa* are sky blue with a yellow eye; *M. arvensis* in bud has a yellow tube with pale pink corolla lobes, which change to blue and finally fade to white; *M. versicolor* is yellow changing to blue and violet, and *M. alpestris* produces dark blue, bright blue, reddish, and even snow white flowers. The flowers are visited by many species of flies. Lithospernum purpureo-cœruleum is at first purple-red and later blue. *Pulmonaria officinalis* is red and later blue-violet. *Echium vulgare* (blueweed) has large, showy, irregular flowers,

which change from red-purple to bright blue. *Symphytum officinale* has a yellowish-white corolla, which is rarely purplish. *Borago officinalis* has a bright blue corolla, with which the black cone of anthers offers a marked contrast. The last three species are fertilized chiefly by bees. To this family belongs *Arnebia cornuta*. When the flowers open each of the five petals is marked with a dark purple spot, which by the third day has faded entirely away leaving the corolla bright yellow. In the Boraginaceæ, it is evident, that yellow and white are more primitive than red, purple, or blue. A change in the cell sap from an acid to an alkaline condition explains the coloration of flowers, which are at first red but afterwards blue. The transition from yellow to blue may be caused by the development of a soluble blue pigment masking the yellow plastids, as in the purple pansy. The species of Boraginaceæ are very rich in anthocyan. The roots and in some instances the leaves and stems, as in Echium and Lithospermum, stain violet the herbarium paper on which they are mounted. From the roots of *L. canescens* (puccoon) the Indians derive a red dye. Another species of this family *Alkanna tinctoria* (alkanet) is extensively cultivated in Europe for its carmine dye used in coloring silk and cotton fabrics, and also oils, wax and wine. In the sheep pastures of New Mexico there grows another species *Plagiobothrys arizonicus*, called blood purslane, "when the sheep find a patch of it, it colors their heads red clear to the ears."[1]

The flowers of the Verbenaceæ are two-lipped. Of the 12 northern species, two are white, two purple and eight blue. The species present various interesting color changes and combinations of colors. The native species of Verbena are white, purple, or blue. The cultivated varieties are remarkable for their brilliant scarlet and crimson colors. *Lantana mixta* from Brazil has flowers, which at first are white changing to yellow, orange and finally to red. According to Fritz Müller, the flowers when yellow are sought by bees, and when red by butterflies. *L. nivea* has sweet-scented white flowers, which in the variety *L. mutabilis* change to bluish. The flowers of Clerodendron are

[1] Norton. *Report Missouri Botanical Garden*, 1898, p. 149.

bicolored with the calyx and corolla strongly contrasted; *C. trichotomum* from Japan has a white corolla and a red calyx, while *C. thomsonæ* from tropical Africa has a snow white calyx and a bright crimson corolla.

The Labiatæ is a large family of about 3000 species of widely distributed plants, which are especially abundant in the region of the Mediterranean. The foliage usually contains an aromatic volatile oil. The flowers are distinctly zygomorphous, and highly specialized both in form and color. In this family and the Scrophulariaceæ the gamopetalous plants come to a secondary culmination. But while these two families belong to the same order they are in different subseries, and are more closely united with other families than with each other. The Labiatæ connect with the Verbenaceæ, both having one-ovuled carpels; and the Scrophulariaceæ are related to the Solanaceæ, both having carpels with numerous ovules.

The 120 species of the Labiatæ contain 24 white, 4 yellow, 12 red, 47 purple and 33 blue flowers. According to the length of the corolla tube and the consequent limitation of the insect visitors, the flowers may be arranged in three groups. In Mentha and Lycopus the tube is short, and the visitors are chiefly flies. In Thymus, Origanum and Betonica bees become of increasing importance, though flies and other insects are also numerous. While Stachys, Ajuga, Teucrium, Salvia, Lamium, Galeopsis are almost exclusively fertilized by bees. Individually the flowers are often inconspicuous and significance is gained by massing. In Mentha and Lycopus the stamens are reduced to four or two, the nearly regular corolla is 4-lobed, and the small, pale purple or white flowers, which are fertilized chiefly by flies, are in dense axillary whorls. These genera have evidently retrograded and departed from the typical labiate form. The flowers of Lycopus are the smallest of this family. The small flowers of Thymus and Origanum are in terminal clusters, 2-lipped with a five-cleft corolla. In both genera there occur large hermaphrodite and small pistillate flowers. The color is purple and the visitors are flies, bees and butterflies, but the largest percentage is of flies. The flowers of Kœllia (Pycnanthemum), or basil, are more or less bilabiate. They are small,

white, or purple-dotted, and for the most part are in terminal clusters. The species, like the mints, are strongly aromatic-scented. In many purple-flowered species of the Labiate family the leaves and stems also develop a purple pigment, as in Mentha and Origanum. The entire plant of the summer savory (*Satureia hortensis*) turns purple in autumn, while on the other hand the white-flowered water horehound (Lycopus) has pale green foliage.

A great number of the larger labiate flowers are chiefly, or almost exclusively, fertilized by bees. A number of species, however, have scarlet flowers and are adapted to humming-birds. The species of Stachys are white, yellow, red, or purple, and the lower lip is frequently spotted or variegated. The flowers are rather large and bees are the most important pollinators. The flower of *S. recta* is yellowish-white with the border of the upper lip marked with two purple stripes, and the lower lip purple spotted. *S. annua* has the corolla tube whitish-yellow with the lower lip red-spotted. The corolla of *S. palustris* is bright purple with a white and dark red marking on the under lip, and the flower of *S. silvatica* is red with a purple and white path-finder on the lower lip. Our four northern species of Lamium are pollenized for the most part by bumblebees. Three are purple or purple-red and one is white. The under lip is variegated. *L. album* is large, white, or sometimes rose-colored, with the under lip pale yellow, marked with olive-colored dots. The pathfinders of the purple-red *L. maculatum* are dark red with white markings, and of the bright purple *L. purpureum*, a dark red flake and dark red lines.[1] The flowers of Galeopsis, or hemp-nettle, display as great a variety of colors. *G. tetrahit*, so common in waste places, is purple with a pathfinder on the lower lip of a yellow spot crossed by a network of red lines; while *G. versicolor* is yellow with the lower lip in front dark violet but at its base yellow. The species of Prunella are also bee flowers; *P. vulgaris* is blue-purple, white, or rose-colored. *Salvia pratensis* is usually purple, but Müller mentions a pink variety grown in his garden. *Ajuga repans* is a bumblebee flower, and also

[1]Knuth, Paul. *Handbuch der Blütenbiologie*, bd. ii, teil 2, p. 259.

has blue, rose, or white flowers. The native species of Salvia are blue, or blue and white, and are fertilized by bumblebees. But in tropical America there occur scarlet and fire-red species, which are visited by humming-birds. Further illustrations of variegation may be observed in Teucrium, Scutillaria, Nepeta and Monarda. It will be noted that the bee flowers are larger and more variable in color than the species to which flies are the most important visitors. Bee fertilization is correlated with high specialization in form and color. Pathfinders usually occur on the lower lip and consist of two, three, or even four colors, one of which is very frequently yellow. The Labiatæ have but four yellow flowers, while the Scrophulariaceæ have thirty-three. These four species are pale or greenish-yellow, as in Lophantus nepetoides. The colors of the Labiatæ will again be considered under the Scrophulariaceæ.

The Solanaceæ, or potato family, belong to the same sub-series as the Scrophulariaceæ, or figwort family. The flowers of the Solanaceæ are regular or nearly so, and the corolla tube varies greatly in length from rotate and campanulate to salverform. There are five perfect stamens of equal length. This family represents an earlier stage of the Scrophulariaceæ. Petunia is a transition form, which has the border unequal and four of the stamens didynamous and the fifth aborted. Many species of Linaria, a well known genus of the Scrophulariaceæ, have been known to become regular.[1] A peloric form of *Antirrhinum majus* is also known. Moreover at an early stage in their development the flowers of the Scrophulariaceæ are regular.

Nine species of the Solanaceæ are white, twenty-one yellow, two purple, and eight blue. The genera Lycopersicum (tomato) and Solanum (nightshade) contain pollen flowers, and are devoid of honey. They are visited sparingly by both bees and flies. The rotate flowers of Solanum are white, yellow, purple and blue with a cone of yellow anthers in the center, or in *S. heterodoxum* the lowest anther is violet like the corolla. The violet corolla of *S. dulcamara* (nightshade) is marked at the base with ten green spots, which Müller observed Syrphidæ

[1] Darwin. *Animals and Plants under Domestication*, vol. ii, p. 35.

examining in search of nectar. The fruits of this genus are green, white, yellow and red. The small, open, campanulate flowers of Physalis (ground-cherry) are nectariferous. The seventeen northern species are greenish-yellow, bright yellow, or sulphur-yellow, sometimes throughout, but often with a brown or purple center, or with purplish spots. The yellow anthers are frequently tinged with purple, and the calyx in some species is purple-veined. The berry is also yellow or purple. In Leucophysalis the flower is white sometimes tinged with purple with a yellow center. The fruiting calyx of the strawberry tomato, *P. alkekengi* from Southern Europe, contains an intense scarlet pigment.

The flowers of Nicotiana and Datura are funnelform, or tubular, and adapted to Lepidoptera. *Nicotiana rustica* and *N. longiflora* are nocturnal species; in the former the corolla is yellowish-green, and in the latter it has a white border and a green tube four inches in length. The common tobacco, or *N. tabacum*, which is a diurnal species, has red-purple flowers. In Datura the large nocturnal flowers are four inches long by two broad. *D. stramonium* has green stems and white flowers, while *D. tatula* has violet-purple flowers and purple stems. *Brunfelsia grandiflora* has greenish flowers two inches in length; while *B. latiflora* has lavender flowers with a white eye, which fade to white. Both of these species come from South America. Two cultivated exotic genera, which also have funnelformed corollas, are Salpiglossis and Petunia. The large handsome purple or rose-colored flowers of Salpiglossis are remarkable for being netted-veined and laced with golden yellow. The numerous hybrids of Petunia under cultivation are chiefly derived from two South American species, one of which is white and the other red-purple. They exhibit a wonderful variety of bicolored, tricolored, and variegated flowers often veined or mottled in endless ways. A unique form is striped or margined with green. The coloration of the Solanaceæ, which is an extensive tropical family, is of more than usual interest because of the many green flowers of large size which it contains. These green flowers, as well as many large white and yellow colored species, are funnelform or tubular, most strongly sweet-scented in the evening and

adapted to night-flying Lepidoptera. Nocturnal fertilization has prevented the development of red and blue colors, as in Cestrum nocturnum with yellowish green, *C. parqui* with dull yellow, *Datura metel* with white, and *D. fastuosa* with the flowers violet outside and white within. *Cestrum elegans* and *Nicotiana tabacum* are day flowers and are rose purple. Of the bumblebee flowers, *Atropa belladonna* is dull purple, and *Hyoscyamus niger* is dull yellow with purple veins. The colors of the rotate flowers of Solanum and Physalis are white, yellow, purple and blue, and are sought by both bees and flies.

Unlike the Solanaceæ the Scrophulariaceæ are most abundant in temperate and arctic regions. There are about 2500 species. Of the 113 northern flowers, 13 are white, 33 yellow, 7 red, 32 purple, and 28 blue. As in the Solanaceæ the number of yellow flowers is much larger than in the Labiatæ. In Verbascum and Veronica the flowers are wheel-shaped. Three of the northern species of Verbascum, or mullein, are yellow or sometimes white. Gärtner made many experiments in crossing the yellow and white varieties, and actually raised one variety from the seed of the other.[1] *V. phœniceum* is purple, rose-colored, or white. When the purple variety of *V. phœniceum* was crossed by the yellow variety of *V. blattaria*, the corolla of the hybird was pale crimson.[2] The leaves of *Verbascum thapsus* are yellowish green, often spotted with yellow, or turning completely yellow. The visitors are a miscellaneous group of insects, of which bees are the most important. Müller devotes considerable space to the consideration of the colors and manner of fertilization of the speedwells, or the genus Veronica. Most species have light or dark blue flowers often with darker stripes; but those of *V. urticifolia* and *V. perigrina* are pink. The flowers, which are small and rotate, with the sepals and petals reduced to four and the stamens to two, have evidently departed widely from the primitive type of the family. The visitors are chiefly flies, especially Syrphidæ, the honeybee and the smaller bees. Müller finds it difficult to explain the origin of the blue coloring by the

[1] Darwin. *Animals and Plants under Domestication.* Vol. ii, p. 83.
[2] Kerner. *Natural History of Plants*, vol. ii, p. 567.

selective influence of the pollenizers, and regards the question of its evolution as still unsolved. It is surprising that he does not give more consideration to the influence of physiological, as well as of ecological causes, in determining the particular colors of flowers. In this genus, as in many others, it is the character of the pigment-forming function, which is of chief importance. On the Alps Müller found *Tozzia alpina* to be also a fly flower. The corolla is bright yellow except that the three lower petals are spotted with dark purple. In view of the fact that fly-flowers are white, yellow, red and blue, the evidence that their particular coloration has been determined by the color sense of Diptera must be regarded as unsatisfactory.

The species of Scrophularia are wasp flowers, green or purplish without and brown purple and shining within. The corolla is short and round with easily accessible honey. By far the greater number of species of the Scrophulariaceæ are adapted to bees and many to bumblebees alone. The species of Linaria are for the most part bumblebee flowers. *L. vulgaris* is bright yellow with an orange-colored palate as a honey-guide, while *L. canadensis* has small blue flowers with a whitish palate. *Antirrhinum majus* is bright purple or white with a yellow palate. *A. orontium*, according to Knuth, is red, or rarely white, with darker red lines. The under lip displays a pale yellow pathfinder and a white zone besides other markings. *Chelone glabra* (turtle head) is white with reddish lips. In Maine this species is fertilized exclusively by bumblebees. *C. obliqua* is bright rose color. *Digitalis purpurea* is purple with dark purple spots within on the lower side. *D. lutea* is yellow. *Melampyrum lineare* is whitish with the lower lip yellow. Other species of this genus have bright yellow flowers. Pedicularis with the flowers yellow and red is also fertilized by bumblebees. *Rhinanthus crista-galli* (yellow rattle-box) is bright yellow with the lower lip purple-spotted.

In a preceding paper the capability of the calyx to develop different colors was shown to equal that of the corolla. In connection with the genus Castilleja the variety of coloring in the floral bracts may be considered with advantage. In *C. coccinea*, or the scarlet painted cup, the flower is greenish yellow and the

floral bracts bright scarlet, or occasionally both bracts and calyx are yellow. In *C. indivisa* both bracts and calyx are bright red, and in *C. acuminata* yellowish or purplish, but in *C. sessiliflora* they are green similar to the leaves. In *Monarda didyma* of the Labiatæ the corolla is scarlet and the bracts red, in *M. media* both are purple; but in *M. clinopodia* the bracts are pale or white, and the flower is yellowish-pink. In *Cornus canadensis* the involucre is white and white or red in *C. florida*. *Bourgainvillea glabra* has three conspicuous purple-red bracts. Finally in the Proteaceæ *Protea globosa* has "the upper foliage leaves grouped into a large outer envelope, which surrounds the spherical golden yellow inflorescence, and these crowded leaves are colored blue in contrast to the lower scantier foliage which has a grass green color." Other illustrations of colored floral bracts occur in the aroids, spurges and Compositæ. The floral bracts evidently may develop as wide a range of colors as the floral leaves, though blue is much rarer.

Müller in his *Alpenblumen* has considered the relation of bees to floral colors at considerable length. In many genera, when the flowers are wheel-shaped and adapted to short-tongued visitors, the species are colored alike, mostly yellow or white, as in Ranunculus and Potentilla, the Alsineæ, Cruciferæ and Umbelliferæ. Even when the honey is partially concealed this may hold true, as in Mentha and many Cichoriaceæ and Compositæ. The short-tongued insects visit these flowers indiscriminately and not infrequently the bees. Genera adapted to bees on the contrary usually display a variety of colors, as white, yellow, red, violet, blue and brown, especially when they bloom in the same locality at the same time. Among the examples given by Müller are *Aconitum lycoctonum* yellow, *A. napellus* blue; *Lamium album* white, *L. maculatum* red, *Galeobdolon luteum* yellow; *Salvia glutinosa* yellow, *S. pratensis* blue; and *Pedicularis tuberosa* whitish yellow and *P. verticillata* purple. An exception to this rule is offered by the Papilionaceæ, which contain a great number of yellow flowers. Here Müller thinks that the color is so strongly transmitted that not even small variations appear, and there is consequently no opportunity for the development of a variety of colors. As a rule, however, genera

with rotate open flowers are monochromatic, while genera with highly specialized corollas adapted to bees are polychromatic. How have these color differences arisen, and how far are they due to the selective influence of bees? That bees in collecting nectar adhere closely in their visits to a single species is well known. Even when the flowers are nearly alike in form and color the honeybee often shows a remarkable power of discrimination. If all of the flowers blooming at the same time in a locality were of the same color, it is evident that bees could not distinguish between them as readily as when there is a variety of colors contrasting with each other. This is the reason of the development, according to Müller, of the numerous color differences in bee flowers. There can be no doubt that bees can distinguish between different hues, and can make their visits more quickly and easily because of the contrasts of flowers in coloration. If, says Müller, we assume that one of two forms, closely allied in structure and of the same color, should vary in color, bees would distinguish it at once, and follow it more easily in their visits. He found, moreover, that a majority of bee flowers are red or blue. Of one hundred species of bee flowers observed by him on the Alps thirty-four were white or yellow, and sixty-six red or blue. In the German and Swiss flora he records that 152 bee flowers were white or yellow, and 330 red, violet, or blue. The honeybee and bumblebees showed a much larger percentage (about 20 %) of visits made to red and blue flowers of all kinds, including not only flowers with the honey partially or deeply concealed but also those with it fully exposed, than to white and yellow flowers. To explain the greater frequency of their visits to red and blue flowers, it does not seem to the writer necessary to assume that they find greater pleasure in these hues. The more specialized bees learn from experience, and it is not difficult to understand that they would soon come to associate with red and blue colors a more abundant supply of nectar and greater freedom from competition.

(*To be continued.*)

THE CAUSES OF ACCELERATION AND RETARDATION IN THE METAMORPHOSIS OF AMBLYSTOMA TIGRINUM: A PRELIMINARY REPORT.

J. H. POWERS.

DURING the past six seasons the writer has been collecting facts on the metamorphosis of *Amblystoma tigrinum*, both by observation and by experiment. It is hoped to publish an extended account latter; but as relatively definite results have already been reached, the interest of the subject seems to warrant the present publication of an outline, giving conclusions and something of the evidence from which they have been drawn.

The extreme variability of our tiger salamander in regard to the time at which it undergoes metamorphosis is well known. Individuals may breed in the larval condition: witness the Mexican Axolotl, which the concensus of scientific opinion has now practically reduced to the rank of a sexually mature larva of our common species. At least one, and probably two, specimens of our common species, male as well as female, have come into the writer's possession which showed every character of the Mexican animal, even to sexual maturity. More striking than these facts, however, are the anomalies of size which frequently occur. My largest larva weighed, before the beginning of metamorphosis, one hundred and thirty-six grams; my smallest adult weighed but three grams. Thus a larva may outweigh an adult in the ratio of forty-five to one. The above mentioned giant larva, while kept in an aquarium, ate daily, for about two weeks, at least one fair sized adult Amblystoma of its own species; some days it ate two, or followed its cannibalistic meal by devouring a piece of liver the size of a man's thumb.

What are the causes which produce these almost unparalleled extremes of variation? Those familiar with the literature of the subject know that many regard the question as already definitely settled: favorable conditions for aquatic life are supposed to

prolong the larval, gill-bearing stage; while unfavorable conditions for aquatic life — *e. g.*, the drying up of ponds, with forced aerial respiration — are thought to be the regular causes of metamorphosis. Heat and light are regarded by many as subsidiary causes.

This explanation of the metamorphosis of Amblystoma — and of allied forms — as due to a direct response to changing conditions of environment is traditional. It has received further support from casual observations of naturalists, who have seen these animals undergoing metamorphosis on the mud of evaporating ponds. But the final sanction which raised the hypothesis into an almost universally accepted datum of science was Weissman's great article, "On the Change of the Mexican Axolotl to an Amblystoma."[1] This article was based upon Marie von Chauvin's experiments with five larvæ only. Later and much more extensive experiments by the same person were much less favorable to Weissman's conclusions. Indeed a careful study of their methods and results seems to the writer rather to cast doubt upon the entire conclusion that enforced air breathing caused the metamorphosis of these supposed Axolotls. But a consideration of these experiments in detail is beyond the scope of the present article. Brief reference will be made to them latter. I will now pass at once to the results of my own observations and experiments, which have been made on Amblystomæ in the vicinity of Crete, Saline County, Nebraska.

First, metamorphosis, in the writer's vicinity, occurs rarely if at all as the obvious result of enforced air breathing through the drying up of ponds. Diligent search has been made; in one summer over one hundred ponds and larger pools were examined. Many contained larvæ; but none were found in ponds or pools that were less than one foot in depth. The last remnants of large ponds, where larvæ had been abundant a few weeks before, showed no trace of them, although the water might be alive with the tadpoles of the common frog. Experiment showed that Amblystoma larvæ could not usually withstand the temperature of very shallow water exposed to Nebraska sunlight in June, while the tadpoles of Rana were unharmed by it.

[1] A translation of this article will be found in the *Smithsonian Report* for 1877.

However, not death, but early metamorphosis is the probable explanation of this early disappearance. Metamorphosis frequently takes place early in the season, even in June. I have taken small specimens in metamorphosis as early as June from ponds with a depth of water from four to six feet. A careful series of observations, in the case of a single pond, showed the period of wholesale metamorphosis to occur, in this instance, in the latter half of August. Yet in this case unusually heavy August rains had raised the pond to its maximum height and even caused considerable overflow. In spite of repeated search at appropriate times and places, no Amblystomæ have been found in metamorphosis on the mud of drying ponds. That they are so found in other localities the writer knows from childhood experience, as well as from report and record. Our ponds are usually too muddy for direct observation, but the constant use of the dip net has shown me that these larvæ undergo metamorphosis in a considerable depth of water, preferably about three feet. My field notes show but few instances of single specimens in metamorphosis taken from the shallow borders of ponds; many more from deeper water, even up to six feet. In but a single instance have I seen an Amblystoma leaving a pond before the metamorphosis was quite complete.

The second point at which I have failed to make my observations tally with the statements of others is in regard to the habit of rising to the surface for air. It has been stated that rising to the surface for air, or at least the more frequent rising, precedes or ushers in, metamorphosis. I have been favorably situated for the observation of this habit, and have followed its beginnings, its sudden acceleration, its slow or still more sudden cessation, rebeginning, etc.; but whatever the significance of this strange and intricate phenomenon may be, it is certain that, with our larvæ, it stands in no immediate relation to metamorphosis. It may begin and, within a day or two, become incessant with larvæ far too small for metamorphosis, under any conditions. I have seen a group of about a hundred large larvæ, in well aerated clear water, ten feet in depth, so incessantly playing to the surface that the water seemed as if rained upon with large drops at the beginning of a shower. Day after day I found them

equally active in the same place; their gills were long and well fringed; not one showed the labored upward ascent or the dead after-sinking which characterize the larva in which metamorphosis has begun. Suddenly, within twenty-four hours, this air-taking at the surface entirely ceased; a half hour's watching showed hardly a swirl. Yet the larvæ were still there; for a few days later, the water being let from the basin, I caught them, not one showing a trace of gill shrinkage. Experiment with larvæ under controlled conditions conclusively confirmed these general observations. Moreover, larvæ in metamorphosis do not rise with especial frequency; and times of rapid surface play have never coincided with times of wholesale metamorphosis.

It has been further said that, just as the bringing of Amblystoma into the air would force the change to the adult condition, so enforced aquatic conditions would prolong the branchiate condition,— larvæ would not undergo metamorphosis if kept in water and unable to crawl out, *e. g.*, if kept in glass vessels with perpendicular sides. Yet several hundred larvæ have undergone metamorphosis in my laboratory under precisely these conditions; not one, in fact, has refused to do so. The form of the aquarium, the accessibility or inaccessibility of a foothold out of the water have exerted no noticeable accelerating or retarding influence upon the duration of the larval state. Indeed, I have thus far been unable to raise larvæ in the laboratory to their maximum size. I have tried hundreds of them, have varied conditions in many ways, and they thrive well, too well, as the sequel will show; but my largest specimen was but 17.7 cm. in length, while, in one instance, I have seen hundreds of larvæ in a pond that exceeded this dimension. Out-of-door experiments, in tanks, cisterns, etc., have, with one exception, to be mentioned later, led to precisely similar results. Larvæ undergo metamorphosis where the possibilities of terrestrial life are not present; they undergo metamorphosis under conditions where larvæ flourish, but where adults slowly die of starvation.

The most crucial proof, it has been thought, of the power of adaptive response in the young of Amblystoma has been the bringing of the young into shallow water or out of the water altogether, that enforced lung breathing might induce the transi-

tion to the terrestrial form. That animals so treated have, in some cases, metamorphosed is certain; but have sufficient control experiments been conducted to eliminate the possibility of other causes than aerial respiration? The writer has repeated these experiments, and does not find that air-breathing, taken by itself alone, is the natural cause of metamorphosis, or even, in all probability, an accelerating condition. I will instance one set of typical experiments.

Five larvæ, 14 to 18 cm. long, placed on mud with but water enough to partially cover them; refused to eat; kept quiet; all began metamorphosis three days later, and finished eight days later.

Second: Fourteen larvæ, same as above, placed in large aquarium with five inches of water; larvæ quiet; not fed. Began metamorphosis four to five days later, and completed same ten to twelve days later.

Third: Twenty larvæ, same size as above, placed at same time, in aquarium with water just sufficient to cover back fin. Took little food; frequently excited and active. Eight showed signs of metamorphosis in three days. Thirteen at five days. All had completed metamorphosis in eleven days.

Fourth: Twenty larvæ, carefully assorted, with one exception, as to size and other characteristics to match the preceding, were placed in an identical situation; but with a depth of one foot of water. They ate well from the start, the eating habit being established before metamorphosis began. Yet three began metamorphosis on the third day; many on the fifth day. And all, with the exception of the one peculiar, broad-headed specimen, almost simultaneously with those in experiment three.

Fifth. Simultaneously with the above, more than twenty larvæ, not assorted as to size, and mostly smaller than the preceding were placed in a large aquarium supplied with running water. They ate readily. Metamorphosis was more irregular; but on the sixth day many had begun the transition, and it was completed in about the same period as with the foregoing.

Sixth. Above fifty small larvæ from the same source as the above, deemed quite unsuitable for experiment, as they had not reached the minimum size at which metamorphosis commonly

takes place, were placed in the stone basin of a fountain. The food supply was scanty or none; but there was more or less shade and a continual spray of cool water. Here, it was thought growth could be delayed and the larvæ kept for later experiment. Yet on the eighth day the astonishing fact was discovered that many were in metamorphosis. And on the fourteenth day three adults, 9.5, 10 and 11 cm. long respectively, were found. Others had probably escaped; as, despite the perpendicular stone ascent of several inches, it was found they could do.

I have instanced this series of experiments, first, because of all I have conducted, it is the most favorable to the received hypothesis. Second, because it will serve to illustrate further points as well. It will be noticed that there is a slight apparent acceleration in the metamorphosis of the five larvæ placed with their backs out of the water; yet some of those in the aquaria with abundance of water began quite as soon and finished but a day or two later; all that were strictly assorted as to size and other characters followed suit very soon, while still more astonishing is the early metamorphosis of the undersized larvæ in cool well-sprayed water of the fountain. The well-nigh simultaneous metamorphosis of these larvæ so soon after the beginning of these experiments indicates that the chief cause of metamorphosis was alike operative in all cases; what this case was will become obvious later in the discussion. In other instances I have had larvæ prove much more resistent to metamorphosis when kept partially or entirely out of water. I will relate one, which is interesting because it was a semi-natural experiment and, in part, on a large scale.

Around the sloping cement sides of a large artificial reservoir frost had raised a strip of plastering, perhaps a yard in width, leaving a crevice an inch or more in depth below it. Until midsummer this crevice had been several feet below water, and here about two hundred larvæ had formed the habit of concealment, their abraded back fins telling plainly that their occupancy of the crevice had not been temporary. When these had reached a length of ten to thirteen centimetres the water in the reservoir was slowly reduced in depth, during a week or more, until, at first portions, and then the whole of the crevice was above the

water level. The larvæ obstinately refused to leave their accustomed shelter; they could obviously have swum out with the receding water, and in most instances could have crawled or even floundered down the incline into the water, as indeed they did, if the plaster sheets were raised and the larvæ poked a little. I disturbed but few of them however; it seemed an admirable opportunity to watch for enforced metamorphosis. Yet, despite the favorable circumstances that the crevice remained moist and that the larvæ were shielded from the direct rays of the sun, within a few days most of them had died. In only two of the survivors could I find any trace of gill shrinkage sufficient to indicate probable beginnings of metamorphosis. Contrast with this failure to respond to enforced air breathing, the case of ten which, two years before, I had netted from this same reservoir; they had been accustomed to an unlimited supply of well aerated clear water; their branchiæ were unusually long; their whole aspect promised (as I then thought; this being near the beginning of my experience with Amblystoma) a long continuance of the gill-bearing stage. The larvæ were placed on Friday P. M., in a large aquarium with perpendicular glass sides, supplied with abundance of the same tap water in which they had developed from the egg. They were excessively refractory and restless; no attempt was made to feed them. On the following Monday morning the astonishing fact disclosed itself that every larva had undergone metamorphosis; every gill-cleft was closed; the remoulding of head and body shape were complete; only the merest trace of tail fin in a part of the specimens, with gill stubs less than two millimetres in length, were left. Cope, in his study of museum specimens, would have reckoned every one of these specimens as adults. Yet the transformation had taken place from larvæ of an unusually piscine type, within the space of sixty hours; and entirely in water which was abundant, cool and well oxygenated. To return to the case of the larvæ left out of water beneath the sheets of plaster.

Finding, about the fifth day, that most of them were dead, I overturned the loose plaster and secured the last twelve survivors, two of which, as I have said, already showed barely perceptible signs of metamorphosis. All of them were placed on a

moist surface, under large split sponges raised just enough to give the larvæ sufficient room. The sponges were kept wet. In this situation the two larvæ which showed signs of metamorphosis when taken slowly completed the change, and one other, one of the smallest in the lot, after weeks of hardihood in what appeared like a most unnatural and unfortunate existence, underwent still more slowly, an abnormal metamorphosis. The details of this metamorphosis and its final results, both of which I have occasionally had repeated under similar circumstances, are very interesting; but I will not discuss them here further than to say that they appear to me to indicate that metamorphosis by early enforced terrestrial life is wholly unnatural to these animals, and, in a state of nature, would seldom produce an adult capable of survival, even if the metamorphosis was itself successfully passed. The other nine larvæ, taken from beneath the plaster and placed beneath the wet sponges, all died, seven of them without showing any signs of true metamorphosis, although several withstood their terrestrial conditions for many days.

At this point and in connection with the last-mentioned larvæ, I wish to protest against what seems to me a careless and well nigh unpardonable misinterpretation of certain very simple facts in connection with larvæ exposed to air. I refer to the withering of the gill-tips and fringes and the like reduction of the dorsi-ventral fin fold. Again and again in the literature of this subject it is evident that observers and experimenters have looked upon these changes as the natural beginnings of true metamorphosis. That a novice should so consider them is natural enough, but how an observer, broadly and minutely conversant with the facts of amphibian metamorphosis could so interpret them the writer is at a loss to know. The organs in question do of course suffer when exposed to the air, even to moist air; their extreme delicacy makes this inevitable. The seven larvæ, which, in the above trial, died before metamorphosis had begun did take on a somewhat dilapidated appearance before they succumbed. The gills were more or less shrunken at the tips and their fringes partially withered; the back fin, too, had lopped to one side like a wilted plant, and its margin was uneven and somewhat withered. But these changes, high

authority to the contrary notwithstanding, bear no resemblance, and apparently no relation, to the incipient changes of normal metamorphosis, in which gill and fin-fold shrink, always, first at the base, and never at the tip; and in which other fully as important though less obvious changes are never wanting to tell that a vital and inner crisis has arrived. As well interpret the withering comb of the frost-bitten fowl as a sign of metamorphosis as the withering gill tips and fin margin of the air-exposed larva.

It has been claimed, in connection with the hypothesis that aerial respiration is the cause of metamorphosis, that a definite relation exists between gill development and the disposition to retain or discard the larval form. Large-gilled larvæ resist metamorphosis, it has been said; small-gilled larvæ do not, but are easily stimulated to change. Moreover, the claim has been made, that the branchiæ themselves develop more or less fully, according to the amount of oxygen in the water in which they live.

If there is any truth in these two corollaries of the received hypothesis, it is certainly not the whole truth, and the observations of the writer have so far failed to substantiate it. The gills of these animals vary much in size in a state of nature, without obvious relation to the oxygen supply of the water. I estimate that the surface for oxygen exchange varies, in larvæ of equal size, as one to twenty. The causes are by no means clear. In general I find, in confinement at least, that rich nutrition and quiet habits produce the largest branchiæ. The finest specimens, by far, that I have ever seen, in this regard, were two larvæ raised, almost from the egg, in a jar holding but two liters of water which was changed rarely. The branchiæ of these two specimens surpassed considerably, both in length of the rami and in length and number of the fringes, the branchiæ of the finest specimens taken from the deep, clear water of the city reservoir; although this latter source does frequently yield long-gilled specimens. Moreover, these two larvæ, despite their superb branchiæ, the wonder of all who saw them, were, none the less, air breathers; they rose, not infrequently, to the surface for air. And, still more surprising from the ordinary stand-

point, these two larvæ were, one after the other, striken by the sudden impulse to change, the great gills withering almost in a single night; they underwent metamorphosis at about fourteen centimeters in length, in the very jar of water in which they had been flourishing as larvæ so surpassingly well. My aquaria have furnished any number of essentially similar cases. Whether or not it be true that oxygenated water develops the large gill, it certainly cannot be too strongly emphasized that the large gill, when developed, is no impediment to metamorphosis. I once investigated a pond well stocked with thriving larvæ which struck me by the meagreness of gill development; the rami were short, and very thin, the fringes likewise, irregular, few and short. A few weeks later the gills had considerably increased in size and general development. Yet it was following this period of gill expansion that rapid metamorphosis began. The expansion of the gills was here doubtless in no sense the cause of the metamorphosis. They may have been essentially unrelated phenomena. It is possible however that a connection existed as follows: The small-gilled larvæ, although having reached considerable size, had still the delicate larval skin well adapted in itself to subserve the purpose of aquatic respiration. Metamorphosis seldom begins until this larval skin has given place to the more or less thickened integument which is to finally characterize the adult. This change in integument is not here considered as a part of the metamorphosis proper; for the larva may change its integument and yet long retain its aquatic form. Yet this change is a necessary preparation for metamorphosis; and it is quite possible that it should render the skin less effective for respiratory purposes. The cutaneous circulalation might even be checked, and a corresponding increase of blood flow to the gills, causing their growth. Certain it is that larvæ with the thickened dermis usually have at least well developed gills, and such larvæ, if the right stimulus comes, are ripe for metamorphosis. I will mention in this connection the surprising fact, developed in the course of several experiments, that the adaptation of these larvæ to entire aquatic respiration stands in no constant relation whatever to branchial development. Many experiments were made to induce metamor-

phosis in larvæ confined strictly to aquatic respiration by nettings, so arranged as to prevent the larvæ from rising to the surface for air. But the surprising difficulty was at once encountered that these larvæ are, all of them, air breathers from a very early stage, and usually cannot, or will not, endure for any length of time complete exclusion from air-taking at the surface of the water. With larvæ of but two centimeters in length, when the development of lungs is but slight, confinement below the surface proved fatal. Even with but two specimens in a large aquarium jar, where they had grown from the egg and thriven in the most natural manner possible, the larvæ repeatedly bored through the netting at night to reach the surface of the water; upon the netting being doubled, one larva still penetrated it, while the other was dead beneath it. This experiment was repeated with many variations in method, but little divergence in result. Larvæ with very large branchiæ, taken from deep, cool, clear water, and introduced singly into a large aquarium freshly filled with the very tap-water in which they had grown would sometimes die of asphyxia in a few hours if prevented from reaching the surface. Such results are very striking. "These animals," said an observer of my experiments, "have gills by the wholesale; but they seem to be mainly for ornament." Not only did the largest gilled specimens succumb when confined beneath the surface of standing water, and sometimes of running water, but they showed no greater ability to live under water than the specimens with the smallest branchiæ that could be chosen. Indeed, when, after many trials, we finally secured two specimens that were indifferent or nearly indifferent to their confinement under running water, neither of them were large-gilled forms, and the one best adapted to this treatment was a very small-gilled specimen. Even specimens in the earlier stages of metamorphosis show little less resistance under this treatment; and in one trial showed even more.

Hand in hand with this inability to live as gill-breathers goes the complete ability to live as lung-breathers, even at very early stages. Seldom, if ever, have my larvæ died of bad or poorly oxygenated water. Over three hundred larvæ, of perhaps two to four centimetres, were, in one instance, transferred directly

from a reservoir where they had grown in pure, deep water, to a single aquarium. Here they lived and throve, although the oxygen of the water was so exhausted that minnows died in a few minutes of asphyxia. Yet the gills of these larvæ remained normal.

If metamorphosis really were caused by enforced aerial respiration, and if loss of branchial surface were a chief factor in the process, both of which are assumed by the common hypothesis, then it would seem to follow as a natural or even necessary conclusion, that cutting off the gills should stimulate to metamorphosis. True, European experimenters on the supposed Axolotl did not find this to be the case; but their failure was explained by the fact that the gills of the Axolotl were quickly reproduced. Besides, the larvæ experimented upon in Europe were resistent to metamorphosis under most conditions. Gill-amputation may have constituted a real stimulus to metamorphosis, and yet one insufficient to bring about the actual change. It seemed to me that our larvæ were much more favorable for the experiment, for they are, most of them, predisposed to early metamorphosis. And, moreover, I have not found that the gills were reproduced with especial facility; weeks may intervene with but little growth, and no specimen in my aquaria has reproduced a gill of normal type; they remain short and truncated.

Yet here again experiment gave practically negative results. At intervals during five days, I removed practically the entire gills from twelve larvæ, a few fringes that were situated on the very gill arches alone remaining. The larvæ were kept in a fair amount of water, which was changed once daily and they fed well. Twelve similar larvæ were treated in a similar manner in every respect except that the gills were not removed. Individuals in both sets soon began metamorphosis, two or three with the cut gills showing a possible acceleration of about twenty-four hours over the earliest specimens in the other lot. This, however, may easily have been accidental, the metamorphosis of the majority in the two lots running an almost exactly parallel course. At the end of the twenty-fourth day, twenty-three out of the twenty-four larvæ, still in the aquaria, had completed the metamorphosis.

One only had proved refractory, not having even begun the change. This was one from which the gills had been removed. Like all the specimens it had thriven and made good growth, yet its gills had grown to barely one third natural size. . At this time the specimen was utilized for an experiment under running water, and, despite its several weeks of life with practically no gills, and the small size at which these organs still remained, it withstood fairly well the confinement under water, dying at the end of the second day just after metamorphosis had begun.

The foregoing facts, together with many more like them, have led me to think that the acceleration or retardation of metamorphosis in our species of Amblystoma, is little, if at all, a question of enforced air-breathing, of gill development, of oxygenated or unoxygenated water. Is it then a question of temperature or of light? Again the answer must be largely negative. Not that the writer would deny to these important agencies all influence. A very low temperature checks all life activities in Amphibia; metabolism sinks to the lowest ebb, and metamorphosis is naturally excluded. Light, too, exerts important influences upon the activities of these animals, and thus indirectly if not directly affects growth; and growth and metamorphosis are intimately connected. But abundant observations show that sudden and early metamorphoses are not produced chiefly by excess of light or heat; while delayed metamorphosis is certainly not alone the result of darkness and low temperature. I will mention the following under light:

Larvæ sometimes attain great size in Nebraska ponds despite their complete exposure to the relatively constant sunlight of our clear summer climate. In the laboratory, the largest larva I have ever reared — 17.5 cm. — was kept in a rather small battery jar exposed to the full light of an east window. Others in the same window metamorphosed at very varying stages of growth. On the other hand, larvæ in dark aquaria have frequently metamorphosed with the utmost readiness. In a long series of experiments on the causes of color variation, larvæ were exposed for weeks before metamorphosis to all possible degrees of light and darkness (not to lights of the different primary colors) and no obvious retardation or acceleration of metamorphosis resulted.

Many larvæ have metamorphosed readily after introduction into the almost total darkness of a closely covered, deep cistern.

As to temperature similar facts may be cited; indeed, many of those already cited are obviously applicable. The instance of prolonged larval growth in the east window is especially interesting, for on several of the hottest days of the season other larvæ, in like jars in the same window, died of the heat. On the other hand scores of small larvæ have undergone metamorphosis in shaded aquaria supplied with currents of cool tap water. The instance, already cited, of the phenomenally early metamorphosis of numerous larvæ in the cool water of the fountain basin may be recalled. Even six small larvæ which I introduced into a tank supplied with a stream of the coldest spring water, heavily shaded with trees and covered with two-inch plank, all underwent the change in the course of a few weeks. In short, these Amblystoma larvæ have, with the writer, proved singularly indifferent to wide variations of temperature and luminosity.

What then does control the metamorphosis? But one cardinal factor in the animal's economy is left, and observation and experiment show it to be the dominant factor in question: nutrition. Metamorphosis is a question of nutrition. Stated more accurately, it may be said that metamorphosis is a matter of metabolism, of anabolism passing into sudden katabolism, as the result, usually, of checked nutrition. Other causes may and do coöperate; but a check to nutrition, previously abundant, is by far the most effective and the most frequently operative.

Liability to metamorphosis at any given time is great, in direct proportion to the prevalence of anabolic change at that time; the certainty of metamorphosis at any time is great, in proportion to the suddeness with which anabolism is converted into katabolism. The larva of Amblystoma is an organism, physiologically, in an unstable equilibrium. Carnivorous, an incessant feeder, capable, under the most favorable circumstances, of growing to a length of eighteen centimetres in eight or ten weeks, the overwhelming anabolic changes which are thus maintained tend, when interrupted, to pass suddenly into their opposite, into katabolism. Large larvæ, fed to the maximum, and very fat, lose one quarter to one third of their weight during

a metamorphosis that occupies but a few days. Some constructive changes take place during metamorphosis; but the changes, as a whole, are plainly destructive. The beginnings of the process, the resorption of fin-fold and gills, are plainly processes of self-digestion of peripheral parts. I have seen cases of early enforced metamorphosis, in which it seemed that this destructive action attacked the periphery, not only in fin and gills, but in the legs as well. Now, without for a moment attempting to explain, fundamentally, the nature of metamorphosis, it is thought, none the less, that the description just given makes obvious its intimate relation with nutrition. Looking at the matter thus from the standpoint of physiological facts, and forgetting for the nonce our teleology both "old" and "new," it becomes probable, *a priori*, that quick starvation will be more effective than enforced air breathing in causing the flabby larva to digest its loose and vascular tissues and take on the more compact form of the adult. I may now summarize, briefly, sufficient evidence to support the conclusion that this is the case.

All of the numerous instances observed of extreme acceleration of metamorphosis have been obviously the result of starvation. The three-gram adult, spoken of at the beginning of this paper, was the result of a small larva, accidentally overlooked, and left for several weeks without food, in a jar of water. The excessively early metamorphosis of nearly fifty specimens in the cool water of the fountain is also a case in point, the three or four larvæ that did not metamorphose made little if any growth during the summer, thus showing the absence of available food supply. Metamorphosis in the tank of cold spring water was likewise attributable to this cause; several of the specimens were under the size at which metamorphosis usually takes place; but there was no visible food supply; and the adults that resulted showed very evident emaciation. Many essentially similar instances have been observed.

But prolonged starvation is by no means necessary to stimulate these unstable organisms to sudden change. With full fed larvæ that have reached the length of thirteen to fourteen centimeters a failure to feed for one or two days is almost certain to be followed by a number of cases of metamorphosis. Even over-

eating, followed by indigestion and bloating, frequently upsets the metabolic equilibrium sufficiently to induce the change, and this even in quite small specimens; the accumulation of gas in the digestive tract causes the animal to float for several days, no food is taken, and by the time recovery has occurred the irreversible gill shrinkage, etc., has set in. A careless observer might possibly interpret this floating at the surface, followed by metamorphosis, as an instance where aerial respiration ushered in the change. There is no occasion for such interpretation, however: the animal floats on one side, with the mouth and entire head under water.

Quite in accord with the explanation here given, and constituting a minor confirmation of it, is the fact observed by myself, and independently by an assistant in my laboratory, that in any lot of larvæ of approximately one age it is not the largest specimens that metamorphose first; but an intermediate size. The smallest larvæ will not have finished certain developmental changes which constitute the preparation for the metamorphosis; while the very largest are usually fat, phlegmatic, anabolic larvæ, which are less easily stimulated to sudden katabolic change. Thus in seven experiments, in each of which three larvæ were taken varying somewhat in length, but all of them between eleven and fourteen centimetres, there was but one instance in which the largest of the three began metamorphosis noticeably in advance of its companions, while in four instances the intermediate or the smallest specimen was notably in advance. Much more striking are the facts noticeable in aquaria containing many larvæ, where a few extra large, anabolic individuals frequently postpone metamorphosis for weeks after many of the smaller specimens have become adult.

In close connection with such facts as those just stated and subject to the same explanation is the fact, which I have noted again and again, that the tendency to sudden metamorphosis is directly correlated with the disposition or temperament of these larvæ. Variable as these animals are, in no way do they show greater differences than in their suceptibility to excitement. One of the first ponds well stocked with Amblystoma that I discovered was filled with larvæ of the usual type, but which had

reached a size that is quite unusual in the writer's vicinity. These larvæ were excessively fat, and so tame that, despite the clear water, they could almost be taken in the hand. The specimens removed to the laboratory were equally phlegmatic there, and underwent metamorphosis little if any sooner than their relatives in the pond. The next larvæ discovered in the same summer, likewise in clear water, were so wary as almost to defy my best efforts with the dipnet, and the excitement of those taken was incessant, even during the usually sluggish period of metamorphosis, which, in this case, followed immediately upon their transference to the laboratory. Restless larvæ have, indeed, invariably, with me, undergone metamorphosis as the result of capture and change of conditions. This exceptionally sudden and rapid metamorphosis is no doubt due to the sudden katabolic changes induced by the excessive activity. Even with larvæ of an intermediate degree of excitability, a portion of the individuals usually metamorphose as the result of removal to new quarters, if they have attained the dimensions, etc., which makes metamorphosis easy. And the writer has been able to discover no reason applicable to all such cases, other than that the shock of new conditions, checking or changing food supply a little, always upsets the accustomed rhythm of bodily functions and thereby opens the way for change.

The facts thus far cited have, in the main, been instances of acceleration of metamorphosis, but if their observation and interpretation has been correct, it follows as a natural expectation that facts of the opposite nature should be forthcoming. If a rich food supply suddenly checked is the common cause of early metamorphosis, then a moderate but constant food supply should postpone metamorphosis, until a maximum larval size has been attained, or perhaps postpone it indefinitely. The experimental verification of this side of the proof has been far more difficult, although final success has been reached in a few cases, and these cases quite confirm the view of metamorphosis here adopted. Moreover, the frequent failures are easily explained. As already indicated, our ordinary larvæ grow rapidly, and tend, in the main, to early metamorphosis, *i. e.*, at a length of fourteen centimeters or less. Excepting occasional larvæ of a special type, to be

mentioned later, the only instances of extra-large larvæ which the writer has met with in nature have been instances of larvæ from late deposited ova, in ponds formed late in the season. Such larvæ may live over winter and grow to a very large size — twenty centimeters — by the next June, when metamorphosis occurs. The common explanation would doubtless ascribe this prolonged larval state to the lower temperature of the fall and spring months. But until experiment has given fuller evidence of the influence of temperature, the writer would lay stress on the meagre but constant food supply. For ponds formed late in the season are poorly supplied with Entomostraca and insect larvæ, which constitute the food of aquatic Amblystomæ.

But to return to experimental data. The larvæ worked with thus far have always been rapidly grown specimens; and to furnish them with an even, sparing food supply in the laboratory has not, so far, been successfully accomplished. To keep a constant supply of Entomostraca is not easy; the substitution of earthworms proves far too stimulating, if the supply be regular; and meat, although they thrive on it, is not better: if chopped fine most specimens get none at all, so stupid are they in feeding, and with larger pieces the result is again a too stimulating or a too intermittent diet. The most prolonged larval growth that has been reached, however, has resulted from regular feeding with meat, usually of single specimens in jars. The great point has been to secure the regular taking of food, and, indeed, regular habits all round.

In one instance, two small larvæ were kept the entire summer and fall on *Lemna minor*, a plant which, curiously enough, these carnivorous larvæ will devour in great quantities, although they obstinately refuse algæ and the like. These two specimens (as well as others similarly fed for a shorter time) made no growth at all on their abundant vegetable diet. When my stock of Lemna was exhausted, in the early winter, they refused other vegetable food, until one died of starvation. The other, supplied with meat, grew rapidly, to a length of perhaps eleven or twelve centimeters, when, after an interval in the feeding, it suddenly underwent the same rapid metamorphosis which might, under similar conditions, have befallen it the June before. I instance

this single case to show that mere delay, mere prolongation of the larval period, does not in itself necessarily hinder metamorphosis. Stimulate the flagging life activities and suddenly check the advancing anabolism, and metamorphosis will follow as easily as had growth been rapid from the egg. The opposite opinion has been held by Marie von Chauvin and others.

Laboratory experiments failing, success in rearing larvæ of the largest size was finally reached in cisterns. Although, here too, success only followed after repeated failure. When larvæ of twelve to fourteen centimeters were introduced into cisterns they invariably underwent metamorphosis as a result of the shock and check in food supply. Very small larvæ, introduced in numbers, betook themselves to wholesale cannibalism, resulting in irregular growth and early metamorphosis or death. But larvæ of six or seven centimeters, introduced into cisterns in small numbers, did, in some instances, establish themselves there with interesting results. Several experiments of this kind have been carried out or are now in progress. In one instance, three larvæ withstood metamorphosis for one, two and three years, respectively. The last was taken from the cistern on the fourth summer, still in the complete branchiate condition, although, from faint signs, it is judged that it would probably have become adult during the summer. It was a male and rapidly approaching sexual maturity, the testes showing the first division of the spermatids. These larvæ attained the size of large adults in about sixteen months, growth, in the cistern, being thus only one quarter to one fifth as rapid as the growth of feral or meat-fed specimens. This slow growth indicates that the food supply was light, and the steadiness of the growth, that it was relatively constant.

As a final proof that the metamorphosis of Amblystoma is due to checked nutrition rather than to respiration of air, it seemed advisable to experiment with these larvæ under water, *i. e.*, to subject them to sudden starvation while quite preventing their coming to the surface for air. As the adult Amblystoma frequently passes hours and perhaps days under water, and as observation had shown metamorphosis to take place normally, in the water, why should not the complete change take place

under water? Marie von Chauvin found that the larvæ of *Salamandra maculosa* would not, at least contentedly, retain its gills under water; but her experiments were not carried to their full conclusion.

The attempts to produce the perfect adult Amblystoma under water were not successful, although they fell little short of success. Advanced stages of metamorphosis were produced; in one instance only a trace of tail-fin and gill-stubs remaining. As already indicated, the great difficulty encountered was the unexpected fact that all of the larvæ are air breathers, no matter how complete the development of the branchiæ. No larva could be found capable of living for more than twenty-four hours below the surface of standing water, no matter how pure, or how large the volume. Their tenacity of life varied much. In a few instances, by repeatedly reviving the semi asphyxiated animal in air, or in running water, and replacing it in well aerated water, under the netting, a partial adaptation seemed to be brought about. Fewer movements were made and no distress or impulse toward the surface would be shown for many hours. But gradual or acute suffocation always occurred sooner or latter. When a small stream of water was let fall directly into the aquarium — in this case usually only a battery jar — the results were better; although many did not live long, when situated even thus, and when the stream was checked, even for an hour, our very best water-breathers always made efforts to reach the surface.

Although complete metamorphosis was not reached under water, yet the theoretical importance of the partial metamorphosis which did result is hardly less than would have attached to the completion of the process. The impulse to metamorphose was plainly present. Over thirty larvæ were tried in running water, below netting; and not one was found, of suitable size, that could there resist the tendency to starvation-metamorphosis. All, which did not die of some other cause, began metamorphosis, usually within six days. Sometimes, indeed, the metamorphosis was begun almost immediately, as if the first shock of transference and partial oxygen-starvation were enough, despite the low temperature, to induce the change. Such individuals, did not, however, survive long; those which carried metamorphosis to

completer stages being such as began slowly, after at least several days of contented life below water.

Before leaving these experiments, I will note that, in spite of their fatal results and the convincing testimony they bear to the inability of these organisms to make complete adaptive response to even moderate environmental change, yet they did seem, sometimes, to indicate, some attempt at adaptive response,— in this case an attempt to retain the branchiate condition. For when the fatal resorption of tissues began, the gills were not, as is usually the case, one of the first organs to be attacked. In some instances they showed no diminution in size or function for several days after the back fin was greatly reduced. Such instances also occur in larvæ in ordinary circumstances; but they are not frequent, and may perhaps, in all cases indicate that a high functional activity of the branchiæ is for a time holding in check the katabolic changes which are elsewhere setting in. Similar observations may be made on the occasional overgrown, giant larvæ, in which the branchial apparatus seems frequently to resist metamorphic processes until other parts of the organism are well under way in the change.

A fairly complete résumé has now been presented of the classes of facts which seem to indicate that the metamorphosis of Amblystoma, if not of all tailed amphibia, has heretofore been, to some extent misinterpreted, and that the chief factors in the process are always sudden shifts in metabolism, usually, or at least most easily, induced by changed food supply. It remains to answer one or two queries that naturally arise, and to indicate one narrow group of cases that, at first observation, seem against the present hypothesis.

In the first place, it may very well be asked, if sudden destructive metabolism is the cause of metamorphosis, why should not air breathing favor the change? It would seem to be favorable to rapid oxidation of tissue. The answer is simple: theoretically it should be favorable, and in very rare instances it may actually be so. The writer has known one single instance of three larvæ which showed astonishing activity when accidentally removed from the water, and they underwent the change rapidly. But in all ordinary cases, larvæ, when quite removed from water or

left in water which but partially covers them, become at once inactive. After a few efforts to crawl, and ineffectual turnings about, as if in search of water again, they "settle down, and wait for rain." This inactivity partially compensates the first effects of starvation; so that these air breathing larvæ may metamorphose even less quickly than similar individuals subjected to starvation, but kept in water which encourages movement.

Second: What of the numerous observations on the metamorphosis of Amblystoma in the air, as the result of the drying up of ponds? Do not these, after all, show that metamorphosis frequently follows the enforced use of lungs? They do, indeed, show that metamorphosis follows the enforced use of lungs; but not that it is caused thereby. A moment's thought will show that this naïve, natural interpretation may well be at fault. As the water of a pond evaporates, what is the first result for these larvæ? Plainly a concentration of their food supply. Insect larvæ and entomostraca, moderately abundant before, become now indefinitely easy of access. The larvæ gorge themselves, for a few days, to repletion. Suddenly the last stages of the accelerating evaporation place them at a disadvantage; freedom of movement is checked, or they find themselves partially out of the water. Experiment shows that under such circumstances the larvæ at once cease feeding altogether. The resulting metamorphosis is obvious, and need be due to no other causes than those which the writer has found effective under experimental control.

It may seem more presumptuous to offer a similar explanation for the results obtained by European experimenters on Amblystoma and interpreted by them in so different a manner. Yet a careful reading of a large part of the literature on the subject seems to the writer to inevitably suggest that many of their results are explicable as above suggested. This is especially the case with the series of elaborate experiments made by Marie von Chauvin. Fearing that her charges would die, as indeed they sometimes did, she always prepared them for the trying ordeal of metamorphosis by raising the temperature of the water in which they were kept (to this she ascribes very great importance),

and feeding to the maximum for several days (to which she ascribes no other importance than giving the animals increased strength). The animals were then brought immediately into water sufficiently shallow to force them, for at least part of the time to breathe air. In this latter condition the experimenter complains again and again that it was next to impossible to induce the Axolotls to take any food whatever. Thus in these experiments, too, we have high feeding followed by practical starvation; and it seems that no control experiments were instituted to determine what the effects of over and under nutrition might have been with Axolotls still in an abundance of water. Yet more interesting is it to note that even the varying degrees of success and failure in inducing metamorphosis in these experiments follow closely parallel to varying factors of nutrition, which factors seem to have been wholly neglected in the final interpretation of the results. *Viz.*, as artificial methods of feeding were developed, earthworms being made to crawl down the throats of the refractory larvæ exposed to the air, it became proportionately difficult to induce metamorphosis by withdrawing them from the water. Even for the space of thirteen months, larvæ whose nutritive equilibrium was thus maintained fairly constant, would sometimes retain their aquatic organs despite their exposure to air.

Before closing, brief reference should be made to one class of exceptional cases of retarded metamorphosis which is of great interest, and which might at first thought, seem to contradict some of the considerations set forth in this paper, while offering, however, no support to the ordinary hypothesis. I refer to certain cases of greatly overgrown larvæ, differing in important respects from the ordinary type. It was one of these that I mentioned as a "giant larva," at the beginning of the paper. I hope later to describe this interesting form in detail. At present I will only mention that it is separated from the ordinary type by its much broader and longer head, with parallel instead of converging sides; its enormous gap of mouth; its flattened or usually concave profile, instead of the even curve of the common larva and adult. It has, besides, unusually heavy limbs, with, in most cases, much flattened toes and webbed feet. These larvæ exceed, by several centimetres in length, the size of even the

largest larvæ of the ordinary type which I have as yet seen. The adults resulting from their metamorphosis are nearly as distinct as are the young. They represent, in many features an extreme development of what Cope has designated the "Western form" of *Amblystoma tigrinum*. But, in the writer's vicinity, they seem to constitute only a very small minority of the species, not more than one out of several hundred.

This form, as already indicated, seems to be very resistant to metamorphosis; it has shown itself so under experiment; and, in ponds where the ordinary form leaves the water at a very small size, these occasional giants may continue in the larval state until they have outgrown all but the very largest adult members of the species. There is thus, in the case of these larvæ, plainly another factor present, in the retardation of metamorphosis. And, as both the mature and the immature stages of this form resemble, morphologically, the perennibranchiate types in several respects, it seems, at present, natural to interpret them as reversions toward a more primitive and perhaps perennibranchiate ancestor.

But although these giant, flat-headed larvæ resist metamorphosis without the especial retarding conditions which usually prevent the change, yet it is to be noted that they, too, undergo metamorphosis in the water, and that high feeding, followed by partial feeding or by starvation will apparently invariably bring about the result. I have taken several giants in the early stages of metamorphosis from deep water; and all the specimens in my possession have finally undergone metamorphosis in aquaria. The branchial apparatus seems more resistant than usual; the whole process takes longer; and the order in which the several component changes occur is different; but the physiological aspect of the process, its causes, etc., remain the same, aside from the matter of delay.

A word, in conclusion, as to the significance and setting of these facts in general theory. The writer does not, with Weissmann, hold that the facts relative to the metamorphosis of Amblystoma or the Axolotl may be sufficient to settle cardinal differences of view in biological theory. The conduct of no one species can be conclusive, or, indeed, more than merely

suggestive, however completely it accords with one theory and discredits another. But if the observations and interpretations noted in this report prove correct for all Amblystomæ, it is evident their bearing on the theory of variation is not unimportant. The variations in metamorphosis of the amphibia in general, and especially of Amblystoma, have been looked upon by many as an excellent example of the direct, purposive response of organisms to their environment. Thus, in the Addenda to his work on the *Batrachia of North America*, Cope quotes a writer who deems these animals plastic and responsive in the highest degree, — metamorphosis and remetamorphosis following upon the predominance of aquatic or terrestrial conditions as if the physiological processes of these animals were gifted with both foresight and free will. Marie von Chauvin, at the close of her last article says: "Es sheint den Axolotln eine eminente Befähigung inne zu wohnen, sich den gerade gegebene Lebensbedingungen anzupassen." The writer has no antipathy to the teleological view of variation, providing facts can be found to demonstrate it. Indeed, observations on Amblystoma were undertaken, with the express purpose of giving, if possible, greater precision to the interpretations suggested by Cope and others. But the facts, as here outlined, all tend to support an opposite view. It may even be said that, in the writer's vicinity, the one representative species of Amblystoma survives for no other reason than that, in its larval condition it can appropriate large quantities of food for which there are few competitors. Its other adjustments, instinctive, physiological, and structural, seem very imperfect. The species is indeed plastic; but not purposive, or approximately perfect in its reactions. And in no particular is this more true than in respect to the various structures and structural changes by which these animals are supposed to adapt themselves to aquatic and terrestrial life.

After all, is not this view borne out by the natural history of the Amphibia in general, with the exception, perhaps, of the more progressive, modern type Anura? A half score of forms become lungless in the adult condition, — a degenerative change of doubtful adaptive value. Cryptobranchus and Amphiuma are permanently aquatic, yet without branchiæ, despite their probable

descent from branchiate forms. Siren and Pseudobranchus, although especially aquatic types, exhibit the strangest anomalies of development and retrogression, of use and disuse of gills.

Many forms of Amphibia develop gills in the egg, or in the intrauterine state, which are destined to serve no purpose in aquatic life, even when an aquatic larval state is soon to follow. Of course there may be more adaptation than we know in these anomolous conditions; but do they, in our present state of knowledge, constitute a proof of adaptation or of direct response to environing conditions?

DOANE COLLEGE,
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THE ORIGIN OF THE SPOROPHYTE.

BRADLEY MOORE DAVIS.

ONE of the most interesting peculiarities of plant life is the striking alternation of generations characteristic of all groups above the algæ and fungi (thallophytes). It is customary to call these two generations by names that indicate the end of their life activities. The gametophyte is the sexual plant, developing the sexual cells or gametes. The sporophyte is asexual, producing spores. These functions of gametophyte and sporophyte have very few exceptions among the higher plants, the latter falling under the head of apospory and apogamy and resulting, at least, in part from abnormalities of environment. The fertilized egg always develops into a sporophyte and the asexual spore, on germination always produces the gametophyte.

The life history becomes then a rhythmical alternation of gametophyte and sporophyte only disturbed when a generation introduces organs for vegetative reproduction and thus makes possible a series of like individuals before the next generation. Such methods of vegetative reproduction by brood organs (gemmæ), buds, bulbs or various fragments are not uncommon in the gametophytes of mosses and liverworts and are very common in the sporophyte generations of the seed bearing plants. Since it is vegetative reproduction and the offspring are literally chips from the parent block they in no way effect the underlying principles governing the alternation of generations.

These principles have become better understood with advances in our knowledge of cell structure in plants, and certain very interesting facts are now known which indicate that the peculiarities of gametophyte and sporophyte are due to structural conditions of the protoplasm that may in a measure be determined. So the problems have become largely an analysis of the events in the cell activities preceding the formation of sexual cells, also at fertilization, and immediately afterward with the development of the fertilized egg, and similarly the period of

spore formation and germination of the asexual spore has been made the subject of careful study. It is evident that the critical periods of the plant's life, when the changes are the greatest, come with the passing of one generation over to the next or in other words at the periods of gametogenesis and sporogenesis with the early developments following each of these processes. We have now an accumulation of studies upon this subject from all three of the great groups of higher plants (bryophytes, pteridophytes, and spermatophytes) and in certain regions the investigations have been numerous. They have uniformly yielded the same results in certain particulars that have established a foundation for some very interesting speculations on the essential differences between the sporophyte and gametophyte.

It will be apparent that these differences must be very fundamental because they are the basis of extensive evolutionary processes with the universal tendency to separate the gametophyte and sporophyte further and further from one another in structure and life activities. From the conditions among the bryophytes in which the sporophyte is so closely associated with the gametophyte as to have been called its fruit by the early botanists, we pass through the pteridophytes to the spermatophytes where somewhat analogous conditions are found in which, however, the relations between the two generations are exactly reversed. Among the seed bearing plants the gametophyte has become so reduced as to live parasitically upon the sporophyte passing its life in the interior of the asexual generation which is thus made the phase that performs the vegetative activities that we expect of plant life. There is no more interesting province of plant morphology than that which traces the evolution of the sporophyte and degeneration of the gametophyte as one passes from the liverworts to the higher plants. There are involved in these processes a number of evolutionary principles of the greatest significance but they do not fall within the range of the present paper.

Can we establish a physical basis for the differences between sporophyte and gametophyte in the cell and nuclear activities during the life history. This has been attempted chiefly through the study of the number of chromosomes present in the nucleus

at the critical periods when one generation passes into the other. The results have been remarkable. The nucleus of the gametophyte generally presents a fixed number of chromosomes as shown in the figures of nuclear division in the various tissues. We may let x stand for this number, which is generally not very large (*e. g.*, 4 in Anthoceros, 8 in Pellia, 12 in Osmunda, 12 in the lily, etc.) The nuclei in the sexual cells (gametes) have this gametophyte number (x). Their fusion, during the sexual act, gives a sexually formed spore whose nucleus has 2x chromosomes, double the number of the gametophyte. This double number (2x) prevails through the entire sporophyte generation up to the time when the sporogenous tissue (archesporium) appears. The events of sporogenesis reduce the number by one half bringing the asexual spore back to the condition of the gametophyte with x chromosomes.

This cycle by which the number of chromosomes is doubled and then reduced probably holds true for all plants above the thallophytes, the conclusions being based upon the study of several liverworts and pteridophytes and a larger number of spermatophytes. The essential facts of the history may be expressed in an abbreviated form as follows.

Gametophyte (× *Chromosomes*) < ♂ gamete × *chromosomes* ♀ gamete > Fertilized egg (2 × *Chromosomes*) — Sporophyte (2 × *Chromosomes*) — Asexual spores (× *Chromosomes*) — Gametophyte.

Reduction of the chromosomes is a phenomenon that has been much studied in connection with sexual processes, especially among animals. It is believed to result from the supposed necessity of keeping the chromosomes in all organisms relatively fixed in number. Since the number of chromosomes is doubled with every nuclear fusion in the sexual act the amount of chromatin would increase indefinitely and in geometrical progression were there not a device for diminishing the quantity at some time in the life history.

If the question is asked why are the chromosomes so important and why should their number be so significant, no answer can be very satisfactory for our deep ignorance of the function of the nucleus is exposed. However, the more detailed the studies upon the structure and activities of the cell the greater

has become the conviction that the chromosomes carry the keys to many and probably the most important problems of development and heredity. We do not know what the chromosome does but its characteristic activities during nuclear division and its behavior at critical periods in the life history are so remarkable that the assumption of its importance in these events is quite justified. The most attractive theory of reduction phenomena assumes that specific characters are largely defined by the amount and nature of the chromatin in the nucleus and that a species, to keep true, must so provide that the chromatin content is relatively stable from generation to generation.

Reduction of the chromosomes at some period of the life history is almost universal among higher animals and plants but we should note an important difference between the two groups in the manner in which this is accomplished. Briefly stated for animals, the reduction occurs just before the formation of the sexual cells (gametes) which have in consequence one half the number of chromosomes characteristic of the organism. The fertilization of the animal egg by the sperm brings the male and female nuclei together and as a result of their fusion the number of chromosomes becomes again normal.

In plants above the thallophytes the history is very different and in sharp contrast to that of the animal. There is no reduction at the time when the gametes are formed. The gametes have consequently the same number of chromosomes as the sexual plant (gametophyte). Their fusion gives to the sexually formed spore double the number characteristic of the gametophyte. This fact is believed to be largely responsible for the peculiarities of the asexual generation that follows. The sporophyte runs through its vegetative development, without any change in the double number of chromosomes, to the time of spore formation when the sporogenous tissue (archesporium) is differentiated. There is then a period of growth during which some or all of the archesporial cells become spore-mother-cells. And during that preparation for spore formation (sporogenesis) the number of chromosomes is reduced by half, becoming again the number of the gametophyte. The reduced number first appears in the nuclear divisions inside of the spore-mother-cell

preparatory to the formation there of the characteristic group of four spores.

It will thus be seen that there can be no genetic relationship between the reduction phenomena of higher plants and animals. They are not found at the same points in the life history and there are also fundamental differences in the details of the process that cannot be considered here.

With these points understood the sporophyte generation takes on new interest in relation to sexual processes in plants for it appears to be a development peculiar to this group of organisms and probably related to a form of sexuality that differs from that of animals in important respects. These differences concern the maturation of the gametes which in animals takes place with a very characteristic process of chromosome reduction and in plants without this phenomenon.

So little is known about the origin of sex in animals that satisfactory comparison with the much better understood history for plants, is not possible. We have already discussed that topic [1] and also sexual evolution.[2]

As there is no reduction phenomena in plants at the time when sexual cells are formed perhaps we find in this fact a clue to the reason of the sporophyte generation and its origin. It must be clear that the most promising line of investigation would deal with the doubling of the chromosomes at the sexual act and the later reduction to the gametophyte number at the end of the sporophyte generation.

The final explanation of the problems can only come through the study of plants below the Bryophytes, that is among the Thallophytes, and we have had as yet very little detailed research on this point. So this paper must deal largely with speculations. We know positively the main facts of sexual processes and chromosome reduction in groups above the Thallophytes but for this group almost nothing.

Nevertheless, we are justified in considering an hypothesis of

[1] Davis, The Origin of Sex in Plants. *Popular Science Monthly*, Nov. 1901, p. 66.

[2] Davis, The Evolution of the Sex in Plants. *Popular Science Monthly*. Feb. 1903, p. 300.

the origin of the sporophyte and its relation to reduction phenomena and this hypothesis may be tested among the thallophytes and must stand this test if the suggestions are to become a theory.

An explanation of the sporophyte upon a physical basis must consider the problem in terms of protoplasmic organization. It must attempt to isolate the structures and qualities given to the egg by fertilization. It must determine the potentialities of the sporophyte generation and also explain why this structure should finally produce spores whose protoplasm returns to the condition of the gametophyte.

The sexual act in all plants above the thallophytes doubles the number of chromosomes. This is the only morphological change that we can observe in the structure of the protoplasm. It is scarcely probable, however, that the doubling of the chromosomes introduces all of the changes that come over the fertilized egg when it takes on the qualities that compel its development into a sporophyte. There is of course the mingling of many substances when the sperm fuses with the egg and we have good reasons to believe that all regions of the protoplasm are effected. But the nucleus gives us the most marked evidence of change in structure and this is shown conspicuously in the number of chromosomes. That the potentialities of the sporophyte are chiefly bound up in the protoplasmic structure of the egg, there can be little doubt. Fertilized eggs of plants above thallophytes cannot be made to develop gametophytes. They are wound up, to use a homely expression, to produce sporophytes and this they will always do under normal conditions. Some peculiar forms that omit certain stages in the alternation of generations are believed to be the products of unusual environmental relations. They are apogamous or aposporous or examples of regeneration and are the exceptions that prove the rule.

The potentialities of the sporophyte generally remain indefinitely long in all regions of the plant where the tissue is embryonic in character, *i. e.*, at all growing points or meristematic areas. These tissues will reproduce the sporophyte or add to its growth as long as they live and retain their undifferentiated character.

But more specialized and older parts of the plant show other characteristics. Some of these regions become specialized for various vegetative activities, assimilation, conduction of water, storage, etc.; some become protective, as the epidermis and cortical regions, and some strengthening. There comes however sooner or later to certain of these older portions another activity, that of spore formation or sporogenesis.

Sporogenesis in the simpler sporophytes generally involves extensive regions of the plant, sometimes almost the entire structure as in certain liverworts (Ricciales). However the evolutionary tendency among higher forms is to develop more extensively the purely vegetative tissues thereby reducing proportionately the spore bearing areas. This very important principle involves the sterilization of sporogenous tissue and may be traced in a very interesting manner as the sporophyte increases in complexity until the sporogenous tissue becomes confined to special organs, termed sporangia. But we cannot consider this topic at the present time.

The significant result for us is the fact that at some period in the history of every sporophyte certain tissues return to the potentialities of the gametophyte and reproductive cells are formed which can only grow into gametophytes. The mechanism, wound up by the act of fertilization, runs down in a figurative sense and the protoplasm, losing its sporophyte characters, returns to the dead level of its ancestral plasm from the gametophyte.

The only evidence of this reversion to gametophyte conditions, as shown by the structure of the protoplasm, is in the reduction of the chromosomes. This occurs just before the sporogenous tissue (archesporium) is ready to form spores. The young cells of the archesporium emerge from their last vegetative division with the sporophyte number of chromosomes in their nuclei. There is then a period of enlargement during which some or all of the cells are stored with a rich supply of protoplasm becoming spore mother cells. During this period of enlargement the reduction phenomena takes place probably by the fusion of the chromosomes in the resting nucleus. The resting nucleus at this period is for some time in the state called synapsis when

the chromatin network is very much contracted, a very conspicuous condition which is not well understood. The first nuclear division in the spore mother cell presents the gametophyte number of chromosomes and this is followed by a second division so that four nuclei result, each of which is destined to preside over a spore.

The fact that the number of spores formed in each mother cell is four appears to have no important morphological significance. It has no connection with reduction phenomena which, as explained above, take place before these divisions. Among the seed plants this division is very frequently omitted in the mega spore mother cells which give rise directly to the gametophyte (embryo sac) thus cutting out a portion of the usual history in the development of spores.

However the fact that four spores are formed in each spore mother cell is interesting because almost universal among the bryophytes and pteridophytes and characteristic of pollen formation in the Spermatophytes. We can see no reason why the number should be four nor is any light thrown upon the problem from our knowledge of the thallophytes.

To summarize this explanation of the sporophyte; we assume that the fusion of gametes (fertilization) gives to the sexually formed spore a different mechanism from the parent gametophyte and this mechanism, under normal conditions, runs a course, producing the sporophyte. The result is a differentiation of the cells through a constant tendency to develop vegetative regions (somatic) in contrast to the reproductive tissue which is proportionally reduced in quantity. The latter (archesporium) generally appears at certain periods of development and in definite regions and represents the return of the sporophytic plasm to the potentialities of the gametophyte. We do not mean to imply that the entire development of the sporophyte is regulated from within, which conception would be ultra preformation. There must be numerous external factors (epigenetic) influencing the vegetative regions and affecting the organography of the plant and certainly the periods of spore formation. But there seems to be the best of evidence that the initial stimulus to sporophyte development comes from within. These are topics that may be

better discussed in a consideration of the evolution of the sporophyte than under the title of the present paper.

The origin of the sporophyte involves the examination of conditions previous to the bryophytes, *i. e.*, among the groups of the algæ and fungi (thallophytes) and we will now consider these.

As is well known the algæ and fungi present organisms far more various in the succession of forms comprising their life histories than the higher plants. There is no general rule of development in this assemblage of diverse groups but rather a number of habits presented by the divergent lines in relation to their various modes of life. In this respect the thallophytes stand in sharp contrast to all plants above the bryophytes. The antithesis of sporophyte and gametophyte, if present at all, is greatly obscured by the intercalation of many and various means of asexual reproduction which may give an indefinite and very irregular succession of individuals. For many years botanists have attempted to define among these lower plants life histories comparable to the alternation of gametophyte and sporophyte. Some of these suggestions appear probable, others have been completely disproved by experimental studies on development.

The test of an alternation of generation involving a gametophyte and sporophyte must always lie with the activities of the sexually formed spore. If this cell invariably produces a phase different from its parent plant then we may properly inquire whether such a structure does not have in itself potentialities that separate it as a distinctly new form of development. It may then be called a sporophyte in contrast to the gamete bearing individual and the succession of generations will be *antithetic* at this point in the life history.

It does not matter how numerous are the successions of generations which depend on various methods of asexual reproduction. They may occur directly before or after the sexual act or over a long intermediate period. Such generations are called *homologous* since they all produce the same form of plant. They do not affect the contrast of gametophyte and sporophyte whenever that change occurs in a life history.

The establishment of alternation of generations among the algæ and fungi depends on the determination of the various

phases as either *homologous* or *antithetic* They are *homologous* when they can be made to develop indefinitely the same form of the plant successively, *antithetic* when the sexually formed spore always gives rise to a distinctly new phase. This test of the conditions in the life histories of the thallophytes is being generally applied throughout the group as opportunities are presented and has led to some interesting results.

Some forms, that at one time were thought to present tendencies towards an alternation of generation, are now known to give merely a succession of homologous phases. The zygospore of the moulds (Mucorales) and the eggs of Vaucheria, the Saprolegniales and probably the Volvocaceæ may on germination produce a series of asexual generations or they may pass at once back to the sexual plant according to the environmental conditions. So there can be no antithesis of sporophyte and gametophyte among these types. These facts have been thoroughly established experimentally by Klebs and illustrate clearly the method by which the problems are attacked. However, the details of the environmental conditions under which such plants become sexual or asexual cannot be given here.

Again, certain thallophytes whose sexuality is highly developed present life histories with but one phase, a sexual plant, and without the least tendency towards the development of a sporophyte generation. Notable examples are found in the Characeæ and Fucaceæ where the eggs on germination produce a sexual plant like the parent. The fact that the oospore of Chara develops a small filamentous structure preliminary to the establishment of the characteristic later growth does not affect the general principle. Investigations on the nuclear history of Fucus report a chromosome reduction after a peculiar manner that cannot be reconciled with the conditions known for groups above the bryophytes. The number of chromosomes is reduced one half just before the differentiation of the oogonium so that the gametes have half the number of chromosomes characteristic of the parent plant. After fertilization the egg has again the regular number and naturally develops into a plant like the parent. The life history may be outlined in this manner.

$$\text{Sexual plant } \underset{\times \textit{ chromosomes}}{} < \tfrac{1}{2} \times \underset{\text{♀ gametes}}{\overset{\text{♂ gametes}}{\textit{chromosomes}}} > \underset{\times \textit{ chromosomes}}{\text{Fertilized egg}} \text{ — Sexual plant.}$$

A comparison of this formula with that given at the beginning of this paper for all plants above the Thallophytes will make the peculiarites of Fucus clear. The reduction phenomena comes at the same period as in animals, *i. e.*, previous to the formation of the sexual cells, and the fertilization of the egg brings that structure back to the potentialities of the sexual plant. In contrast to Fucus, the conditions among the Characeæ appear to be very different. Investigations here have failed to establish a reduction of the chromosomes at the time the gametes are developed. We do not as yet know where the process occurs in this group.

These conditions in Fucus are unexpected and cannot be easily brought into sympathy with the processes of gametogenesis as illustrated in the higher plants. It is the only form among the thallophytes in which the count of the chromosomes has been made for the life history, and until we know the conditions in some of the other types it must remain a puzzle. We are quite in the dark as to its significance in the general problem of sexual evolution among plants and in its relation to alternation of generations. It may present an exception to the usual history of chromosome reduction among Thallophytes and this is to be hoped as otherwise further studies may greatly complicate the problems and require a reconsideration of the theories of the evolution of sex in plants and the origin of the sporophyte.

There are left several groups of thallophytes which are generally supposed to present phases in their life history that are either true sporophytes or indicate tendencies in that direction. The most pronounced evidences of a sporophyte generation are furnished by the red algæ (Rhodophyceæ), Coleochæte and the Ascomycetes. Tendencies in the direction of such alternation of generations are probably shown in Œdogonium, Sphæroplea, Ulothrix and the Conjugales.

The sexual reproduction of the red algæ presents peculiarities that have puzzled investigators for many years. The female gamete (carpogonium), after fertilization, gives rise to a more or less complex system of filaments that always remain attached to the parent sexual plant and in many forms are undoubtedly dependent upon it in part for nourishment and protection. Portions of these filaments and sometimes almost the entire struc-

ture become spores which on germination develop the sexual plant. In 1898 Oltmanns presented the suggestion that the filamentous growth from the female gamete was a true sporophyte. Although we lack the confirmation required by the close study of the details of nuclear activities, nevertheless the theory is very satisfactory especially in its explanation of certain peculiarities of this interesting process of development.

The simplest sporophytes among the red algæ are illustrated

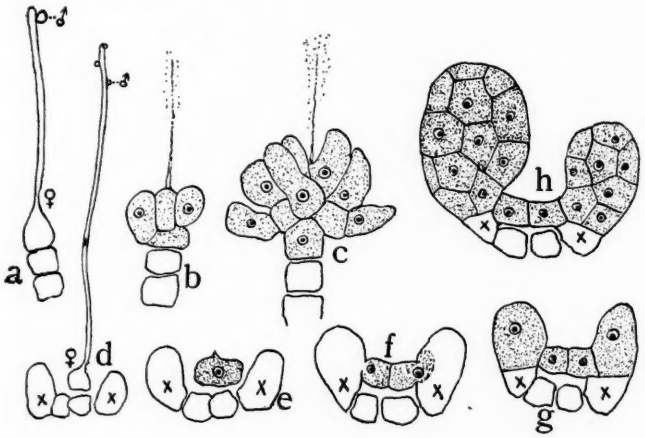

FIG. 1. Semi diagrammatic illustrations of supposed sporophyte of the Rhodophyceæ; shaded structures sporophytic; (x) auxiliary cells; *a, b, c*, Nemaiion; *d, e, f, g, h*, Callithamnion.

by such forms as Nemalion (See Fig. 1, *a, b, c*) and Batrachospermum. Here we have a cluster of short filaments many or most of whose cells become spores. But among the higher red algæ the conditions are greatly complicated by certain cell fusions between the sporophytic growth and the filaments of the sexual plant (gametophytic). Certain cells of the gametophyte are set apart as large richly nourished auxiliary cells whose functions are to assist the developing sporophyte. The fusion of the sporophytic filaments with the auxiliary cells stimulates the growth of the former. It was at one time supposed to be sexual in character but is now believed to be for nutritive purposes alone. Apparently there are no nuclear fusions in these unions of cells but only the mixing of cytoplasm with its

opportunity for the extensive transfer of food material. The main points in this interesting process are illustrated for Callithamnion in Fig. 1, *d*, *e*, *f*, *g*, *h*.

The sporophyte of the red algæ holds a relation to the gametophyte somewhat similar to that in the bryophytes in as much as it is always attached to the latter generation. The sporophytic growth accompanied by developments, usually protective, on the part of the gametophyte constitutes the so-called cystocarpic fruit of the Rhodophyceæ. It should be noted, however, that this sporophyte does not exhibit the upward evolutionary tendencies towards independence so characteristic of the higher plants but rather a degree of dependence approaching parasitism.

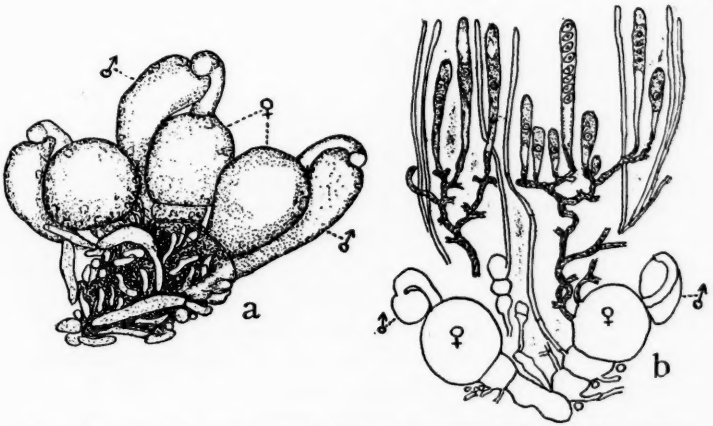

FIG. 2. Pyronema: a, Group of gametes; b, diagram of ascogenous hyphæ (shaded) in relation to the gametes and sterile mycelium of the sexual plant. (Somewhat modified after Harper).

The Ascomycetes furnish conditions somewhat similar to the Rhodophyceæ but here also we lack precise knowledge of nuclear structure at important periods of development. The female gamete, called here the ascogonium or archicarp, develops a system of filaments (ascogenous hyphæ) so closely associated with the parent organism that they can only be distinguished through special staining processes.

The ascogenous hyphæ develop asci, a form of sporangium

peculiar to the Ascomycetes, which are generally associated together and surrounded by an envelope thus constituting a fruit called the ascocarp. These conditions are illustrated somewhat diagrammatically in Fig. 2 for Pyronema, the form perhaps most completely studied.

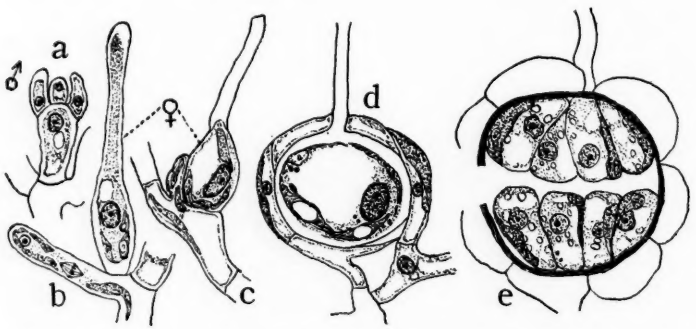

FIG. 3. Coleochæte: *a*, Group of antheridia; *b*, oögonium; *c*, fertilized egg; *d*, oöspore in cellular envelope; *e*, germinating cöspore showing tissue in its interior (sporophytic). (After Oltmanns.)

Coleochæte is a type upon which those who believe in a sporophytic generation among the thallophytes lay great stress. The principal reason for this emphasis is a certain resemblance in form between a cellular body developed by the fertilized egg and the simple sporophytes of the lower bryophytes. As is shown in Fig. 3, *d* and *e*, the fertilized egg after a period of rest develops in its interior a tissue each of whose cells gives rise to a zoöspore which on germination produces a sexual plant. This structure is very suggestive of the sporophyte of the simplest liverworts (Ricciales), but we know nothing about the chromosome history during its development. It is not safe to relate the liverworts to Coleochæte because the sexual organs are so different, for the archegonium is an organ that can hardly be derived from so simple a structure as the unicellular oögonium. However we can readily conceive the Coleochætaceæ as a group tending to develop a sporophyte generation along somewhat parallel but totally independent lines from the Bryophytes.

Coleochæte is generally cited as the Thallophyte in which a sporophyte generation is most evident but in reality the develop-

ments from the female gametes in the red algæ and the Ascomycetes are far more elaborate and show a much higher grade of structural evolution. But the fact that the apparent sporophytic tendencies in these latter groups are long divergent lines related to the peculiarities of their modes of life and so very unlike that of the bryophytes has not given them the degree of attention in relation to the general problem that they deserve. If future studies upon their nuclear conditions support the theory of their sporophytic nature these structures should be cited as the highest forms of sporophyte among the thallophytes but of course in groups very far removed from the main line of ascent to the bryophytes.

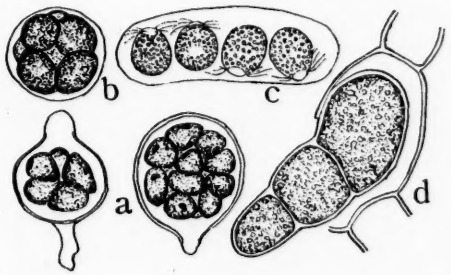

FIG. 4. Germination of the sexually formed spores of *a*, Ulothrix; *b*, Sphæroplea; *c*, *d*, Oedogonium. (*a*, after Dodel-Port; *b*, Cohn; *c*, Pringsheim; *d*, Jurany.)

There are left several algæ somewhat similar to one another in the behavior of their oöspores on germination, and the peculiar group of the Conjugales. The fertilized eggs of Ulothrix, Sphæroplea and Oedogonium (see Fig. 4) generally give rise to several zoöspores which develop into filaments like the parent plant. There is thus a short period after the stimulus of the sexual act when the protoplasm of the organism behaves differently from its usual vegetative activities. Some botanists consider this behavior the beginning of a sporophyte generation introduced after and the direct result of the sexual act. The union of gametes is supposed to give a product (the sexually formed spore) whose protoplasm has potentialities different from the parent plant. There is in general a greater vigor and prob-

ably a modified structure which demands some other form of expression than the vegetative activities characteristic of the species. Such a phase, intercalated after a sexual act, would start its peculiar period of activity because the protoplasm had a different chemical and physical composition from that of the parent plant. Its fundamental characteristics are therefore performed through the fusion of the gametes.

This view of the origin of the sporophyte as primarily the result of sexuality carries with it a comprehensive definition of the phase. It becomes a generation, always intercalated after the sexual plant, which is called a gametophyte by way of distinction. It is a generation always *antithetic* with the gametophyte because of potentialities within itself. When once thoroughly established, the sporophytic generation would be expected to have the power of developing the gametophyte only after it had passed through its characteristic history. The sporophyte could never be an *homologous* generation with the gametophyte in the way that succeeding generations of Thallophytes by asexual methods of reproduction are homologous with one another.

We should not expect the sporophyte to have arisen with the potentialities of immediate and extensive growth developments but rather as a small beginning such as may well be illustrated in Ulothrix, Sphæroplea and Oedogonium. Here the peculiarities of the sexually formed spore seem scarcely more than an increased vigor that expresses itself in the formation of a number of reproductive cells. However, we know nothing of the nuclear activities in these forms and the assumption that the protoplasm of the sexually formed spore is structurally different from that of the gametophyte is speculation but seemingly reasonable. As has been stated, there are several thallophytes whose sexually formed spores develop directly into the sexual plant and indeed the egg of Oedogonium has been known to grow directly into a filament (Fig. 4 *d*). These forms must also be studied in comparison with the types in which the sporophyte generation seems well established.

The Conjugales present some interesting conditions. The union of the gametes gives a zygospore (see Fig. 5 a) that finally

contains a single nucleus although the fusion of the gamete nuclei is sometimes greatly delayed. The fusion nucleus divides into four nuclei previous to the germination of the spore but some of these degenerate. Thus in Spirogyra three nuclei break down so that only one is left at the time when the new filament ruptures the spore wall. In certain desmids (see Fig. 5) two of the original four nuclei degenerate and the remaining two enter into the formation of the pair of new desmids developed in each zygospore. It may be suggested that the division of the fusion nucleus apparently wasteful of material represents the expenditure of energy infused by the sexual act and consequently a sporophyte activity which is necessary to bring the protoplasm

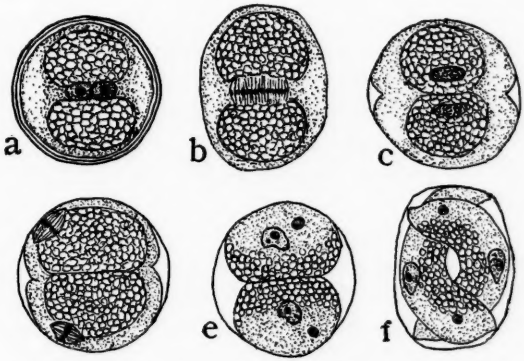

FIG. 5. Germination of the zygospore of a desmid (Closterium). (After Klebahn.)

back to the potentialities of the parent organism. But again we do not know the structural changes that take place in the nucleus of the Conjugales at and after the time of fertilization. Certain diatoms present activities resembling in some respects the Conjugales but the conditions are too complicated to be given here.

This attitude towards the significance of the nuclear divisions following the sexual act is the keystone to the theory of the *antithetic* origin of the sporophyte and its significance, a view held by many prominent botanists including Bower, Strasburger, and Klebs. The sexual act is assumed to give to the fused gametes an organization that will always tend to differ from that

of the parent plant. When the modification is sufficiently great we should expect a new or modified morphology in the resulting generation which would naturally react in a different manner to its environment. The new generation becomes then a phase intercalated after the sexual act and antithetic with the sexual plant (gametophyte).

In its earliest beginnings the sporophyte might differ so slightly from the gametophyte in its potentialities for development as to give no very decided results. Such expressions would be an indefinite cellular body such as is illustrated by Coleochæte or perhaps nothing more than a stimulus to develop several reproductive cells as may be observed in Ulothrix, Œdogonium and Sphæroplea.

An extensive elaboration of the sporophyte generation must follow from any changes that lead to complexity either of external conditions or internal structure through the mixing of protoplasm in the sexual act. The character of the evolution must depend largely upon the environmental relations, so that sporophytes should be expected to diverge in structure from their first inceptions. The most elaborate sporophytic developments in the algæ (*e. g.*, probably the Rhodophyceæ) cannot be like those of land plants, and those of fungi must be expected to present peculiarities of their own (Ascomycetes).

In closing we may summarize the principles that we have discussed in relation to the sporophyte.

First: Its origin, a phase intercalated after the sexual act because the fusion of gametes gives a protoplasm structually different from that of the sexual plant (gametophyte).

Second: Its establishment as an *antithetic* generation through these peculiarities of protoplasmic structure that tend to express themselves in morphological developments different from the gametophyte, which developments are at all time influenced by environmental relations.

Third: Its end, the production of asexual spores with the potentialities of the gametophyte through a structural change in the protoplasm by which the sporophytic characters disappear and the ancestral qualities of the gametophyte again assert themselves.

The sporophyte will vary in complexity with the environmental conditions and the tendency must be always towards structural divergence. There are several well defined and very important principles responsible for these complexities and they will be considered in future papers dealing with the evolution of the sporophyte.

UNIVERSITY OF CHICAGO.

NOTES AND LITERATURE.

ZOÖGEOGRAPHY.

The Atlantis-problem has been re-investigated from the zoögeographical side by Dr. R. F. Scharff.[1] Examining the land and fresh-water faunas of the present Atlantic islands (Canary islands, Madeira, Azores), he arrives at conclusions opposite to those of Wallace. Although he does not deny that there are instances which are apparently due to colonization of these islands by animals transported by winds, currents, etc., he is of the opinion that a large percentage of the fauna indicates that we do not have to deal with truly oceanic islands, but that they once were connected with present continents. He shows that there is reason to conclude that "Madeira and the Azores, up to Miocene times, were connected with Portugal; and that from Morocco to the Canary islands, and from them to South America stretched a vast land which extended southward certainly as far as St. Helena. This great continent may have existed already in Secondary times, as Dr. Ihering suggested; and it probably began to subside in early Tertiary times." Scharff further believes that the northern portions of this latter continent persisted until the Miocene, and that subsequently, in early Pleistocene, there was again a connection of the Atlantic islands with the Mediterranean countries (Africa and Europe).

These ideas admirably agree with those recently set forth by Ortmann,[2] at least as far as it concerns the connection of West Africa with South America, and it is quite interesting that both authors arrived at the same conclusions, as did others before them, namely: Suess (1888), Neumayr (1890), and von Ihering (1891).

A. E. O.

Zoögeographical Development of the Indo-Australian Archipelago has been made the object of a special investigation by Professor Max Weber[3]). He arrives at certain very important conclu-

[1] Scharff, R. F. Some remarks on the Atlantis Problem, in *Proc. R. Irish Acad.* vol. 24, sect. B, part 3, 1903, pp. 268–302.

[2] *Proc. Americ. Philos. Soc.* vol. 41, 1902, p. 348, ff.

[3] Weber, Max. *Der Indo-australische Archipel und die Geschichte seiner Tierwelt.* Jena, Fischer, 1902. 46 pp., map.

sions, which seem well supported, at any rate they are better supported than the previous very general theories concerning these parts. We may summarize them here as follows.

1. We are to abandon Neumayr's theory of a large Jurassic Sino-Australian continent. Sufficient evidence has been brought forward to show that at least a large part of the present Indo-Australian region was covered by sea in Jurassic times, and, moreover, that this sea was by no means a shallow one.

2. Zoölogical evidence supports the view of a continental connection of Asia and Australia during Cretaceous times. As to the size and shape of this connection we possess hardly any indications: we know that certain parts of the Archipelago were land during this period, while marine deposits are known from other parts.

3. During the Cretaceous, and pre-eminently so during the Tertiary, this region was characterized by frequent changes, but during all these times it was a region if not of continental character, certainly of that of a shallow sea with many islands.

4. Wallace's line, a depression between Borneo and Celebes, and said to be continued between Bali and Lombok, does not exist as a zoögeographical boundary between Asia and Australia. Between Bali and Lombok, it does not exist at all, the sea being very shallow there. There is indeed a depression between Borneo and Celebes, but this does not separate Asiatic and Australian faunal development Celebes possessing Asiatic elements in a high percentage. Nevertheless, Wallace's line holds good for a separation of Celebes from Borneo, the former having received the oriental constituents of its fauna not from Borneo, but from the Philippine islands.

5. The three larger Sunda islands (Sumatra, Java, Borneo) were connected with one another and with the Asiatic continent in Pliocene times. The separation of these islands was not contemporaneous: Java was isolated first, and Sumatra last.

6. Borneo was also united, at about the same time, with the Philippine islands and South China.

7. The smaller Sunda islands (Bali, Lombok, Sumbawa, Flores) form a continuation of Java, possessing a fauna which in part is Oriental, and in part Australian. The Australian elements possibly arrived by way of Timor, which shows closer affinities to Australia, and, no doubt, once was part of this continent.

8. Celebes was always separated from Borneo (beginning in the Miocene), but it was connected with the Philippine islands on the one side, and with Java and the smaller Sunda islands (Flores) on

the other. This accounts for its oriental elements. It possesses also an eastern (Australian) faunal element, and this is explained by a former connection by land with New Guinea by way of the Sula islands, Buru and Ceram.

9. New Guinea, Aru, and Ki islands once formed part of the Australian continent in Tertiary times. Temporarily connected with this were the islands of Ceram, Misol, Waigeu, and Halmahera. The Banda sea is a depression formed in Miocene times.

The general conclusions of M. Weber are given by himself in the following words (translated) (pp. 41–43):

"In Pre-Tertiary, possibly in Cretaceous times, Asia and Australia were connected by a land mass. Eurasiatic types of animals popuated this land, which subsided during the Eocene, and was dissolved, into a southeastern portion: present Australia and New Guinea where Monotremata, Marsupials, and ancient types of other groups of animals were preserved, Cassowaries, Birds of Paradise developed, while groups or universal distribution, as for instance Woodpeckers and Sparrows, were not able to reach these parts. Toward the North, a shallow coral sea extended, in which a few elevated parts were present as islands, and possibly offered a refuge to a few older forms of life like Cuscus, primitive Rodents, Insectivors, and others.

"Important changes took place in the Miocene: on the one hand deep depressions were formed in the shallow sea, and on the other hand stretches of land became dry, like Celebes, while in the western parts continental conditions were formed, which offered opportunities for the dispersal of Asiatic animals, such as we know from the Siwalik beds of India. Meanwhile new changes of level took place within this unstable part of the earth's crust, which brought about, by the end of the Pleistocene, the present configuration of the archipelago. These processes caused the local disappearance of that old Tertiary fauna, with the exception of a few relicts, while the immigration of modern Asiatic types was favored. This immigration was of longest duration for the greater Sunda islands, of which Java was the first to become isolated. The fauna of these islands, consequently, resembles most that of Asia. Toward the East, a mixed fauna prevails, and the Asiatic types disappear gradually in this direction, while Australian types become more frequent. This mixed fauna forms a broad transitional zone between the greater Sunda islands and the Philippines on the one side, and Australia, including New Guinea, the Aru and Ki islands, on the other. The faunal elements of this region are of different origin. Celebes preserved

some older Asiatic types, which came probably by way of the Philippine islands. Younger Asiatic immigrants arrived in Celebes by way of Java, and the smaller Sunda islands, but not directly from Borneo, the old Strait of Makassar separating it from this island, which also received immigrants from the Philippines, and sent others in turn to them, from whence they were able to find their way to Celebes.

"In addition, the fauna of Celebes received Australian types from the Moluccas, where they were in part relicts, in part later immigrants from Australia. Possibly also the smaller Sunda islands received a few immigrants from this latter continent."

A. E. O.

BOTANY.

Influence of Light and Darkness on growth and Development.[1] — In this work is presented one of the most important, if not the most important, single piece of research in plant physiology yet published in this country. It is a record of a series of extensive experiments covering several years (1895–1902), from which important generalizations have been drawn. Heretofore too much of the general principles laid down regarding the influence of light upon plants has been based upon experiments with a comparatively limited number of forms. It was the author's intention to avoid these errors and for this reason he selected representative plants covering a wide field in both relationship and form. No fewer than ninety-seven forms were experimented with, and etiolated for an often long period of time. These forms include very diverse orders of plants and comprise practically every form of the plant body of importance. Various typical and modified forms of stems, including those of succulents and xerophytes, the different types of foliar organs and various floral structures were investigated. A very careful and detailed account of the histology of the different etiolated tissues, in comparison with the normal, is also included.

[1] MacDougal, D. T. The influence of Light and Darkness upon Growth and Development. *Memoirs New York Botanical Garden.* vol. ii. Jan. 20, 1903, pp. i–xiii,—1–319, 176 figures.

As might be expected such an exhaustive investigation of the relations of plants to light and darkness, leads to new and interesting conceptions as to the action of illumination in determining the growth of the shoots of plants. It is in this of course that the chief interest of the work centers. As a record of careful and interesting observations the first and major part of the work is of great value, but without entering too greatly into detail, it is impossible to give a fair idea of its contents. For that the paper itself had best be consulted. In passing, the following plants, unusual at least from the standpoint of etiolation experiments, may be mentioned, *Amorphophallus rivierii* Dur., *Bowiea volubilis* Harv., *Cocos nucifera* L., *Ibervillea sonoræ* Grev.— and two sarracenias.

In discussing the theories, hitherto presented, the author points out how inadequate and unsatisfactory the explanations of etiolation phenomena have been. Under the heading "Morphogenic Influences of Light and Darkness" the author expresses his own understanding of the problem by a careful analysis of the facts, and the following is intended to give the substance of his discussion.

Etiolation is not to be regarded as an adaptive modification on the part of the plant, and the form that it assumes in darkness is not due to an effort to reach the light. The various phenomena of etiolation are of course, in the first instance, due to the absence of light, but it is only in some cases that a beneficial modification results. Aside from the absence of chlorophyll, the basal fact connected with the condition of etiolated organs is that their tissues do not show the same degree of morphological differentiation as do those of the normal. This lack of differentiation, and the abnormal increase in size which accompanies it, is most noticeable in the large parenchymatous tracts of tissue. An incomplete deposition of aplastic material allows of a much longer growth period. In this connection the author points out that in organs where extension is possible by the formation of additional parenchymatic cells we have the familiar elongation and enlargement of etiolation, whereas in cases like those of dorsiventral leaves, where the mechanical elements are prerequisite for the expansion of the lamina, the organ remains small. A comparison of normal and etiolated plants shows that growth and differentiation are not only independent phenomena, but are easily separable.

From this point of view then the phenomena of etiolation rests upon the absence of the morphogenetic influence of light, or rather as the author modifies it in considering the effect of continuous illumination in producing partially elongated forms, we may suppose that

the alternate action of light and darkness constitutes the stimulus which finds expression in tissue differentiation. As is pointed out we can very well imagine in the case of continuous illumination, that the plant having adapted itself to this condition ceases to respond so readily to the stimulating action of light. It may be narrowed down then to the fact that it is light which acts as the stimulating influence in inducing morphological differentiation and in its absence the tissues tend to remain in a more or less primitive condition. The action of light, however, is not necessarily direct, since the stimulative influence may be received by one portion of the body and transmitted to another, as is shown by local aetiolation. The author speaks of the enlargement of certain dorsiventral leaves brought about in etiolated plants by the removal of concurrent organs and mentions that even in their enlarged condition they do not show much tissue differentiation, but he hardly explains the reason for this behavior. Possibly this might be regarded as a reaction to the untoward stimulus of wounding.

The total amount of growth or increase in volume, that may be accomplished by the shoot in the expansion of its imperfectly developed tissues during etiolation, is subject to great variation. In many cases the total length, diameter, and volume may be actually less than in a normally grown plant, and indeed the rate of growth need not be so rapid. It may be said that light does not directly affect the rate of growth, that it does not exert the retarding or paratonic influence commonly ascribed to it. This is shown by the action of plants exposed to continuous illumination.

It will be seen that this is an important addition to our knowledge of the influence of light on the growing shoot. Never before has this point of view received such a comprehensive treatment or been supported by such a wealth of facts. The author's insistence that etiolation is not an adaptive reaction and the stress laid upon the anatomical conditions presented by etiolated organs, leads to a far clearer understanding of the actual influence of light as a morphogenetic stimulus. In this latter regard the evidence afforded is especially convincing. It is not yet clear of course why light should so affect tissues as to practically shorten the period of their meristematic condition and to induce the formation of what is usually termed "permanent" tissue. It is said that the aplastic material is not so readily laid down in the absence of light, a statement which suggests a chemical explanation. The exact nature of the chemical changes which are supposed to take place in the differentiation of the usual

forms of tissue, must of necessity remain obscure for a long time to come.

In conclusion the very copious index should be mentioned, in which the novel and withal convenient practice has been adopted of entering author's names with a full bibliography.

H. M. R.

A Popular Introduction to Forestry. — Professor Filibert Roth, formerly of Cornell University, and now, as chief of the Division of Forestry, U. S. Department of the Interior, in charge of the work in the Government Forest Reserves, has just published "A First Book of Forestry."[1] The little volume is intended for use in the public schools and in country homes, and gives in non-technical language, an exceptionally clear and readable account of some of the significant aspects of forest life and growth, the most important principles underlying the practice of forestry, and the methods now employed in such common forestry processes as thinning the wood-lot; seeding for succession; sowing cleared areas: harvesting the wood crop; protecting the forest from fire, insects and fungus pests; and so on. He makes clear the forester's aim so to harvest each wood crop as to speed its successor, and discusses the six principal methods of accomplishing this. Following these accounts of forest life and forest reproduction and the description of the ways in which forests should be protected and helped to make their best growth, he also tells us some of the indirect benefits of forests, such as the protection of soil and conservation of moisture, and gives us a brief description of our own forests, and a history of forest culture from the times of the Romans. Then the structural features and physical and chemical properties of wood are taken up; and finally, a key is added for the determination of our common trees by characters of leaf, wood and bark, and the several valuable appendices in addition to more technical tables include a convenient reference list of the more important woods and trees of the United States. The illustrations, which are excellent in themselves and admirably related to the text, add greatly to the latter's value. As a popular educator calculated to render more intelligent the growing sentiment in favor of forest protection, this little book should have a wide circle of readers, and its usefulness will hardly be less because of the considerable number of other good books recently published by our American foresters.

J. S. P.

[1] Roth, Filibert. *First Book of Forestry.* Boston. Ginn and Co., 1902. 12mo., 291 pp., illus.

Notes.— *The Botanical Gazette*, for February, contains the following articles: — Copeland, "Chemical Stimulation and the Evolution of Carbon dioxide"; Sargent, "The Genus Cratægus in Newcastle County, Delaware"; Long, "The Ravenelias of the United States and Mexico"; Billings, "Chalazogamy in Carya olivæformis"; and Cotter, "Selected Notes."

Rhodora, for February, contains the following articles: Harvey, "An Ecological Excursion to Mt. Ktaadn"; Sargent, "Recently Recognized Species of Cratægus"; Fernald, "Andromeda polifolia and A. glaucophylla"; and Knight, "Some plants new to Maine."

Rhodora, for March, contains Bacon, "An Experiment with the Red Baneberry"; Cushman, "Desmids of Bridgewater, Mass."; L. O. Eaton, "Orchids of Chesterville, Me."; Rand, "Observations on Echinodorus parvulus"; Robinson, "Generic position of Echinodorus parvulus"; and Fernald, "A New Bidens from the Merrimac Valley."

The *Bulletin of the Torrey Botanical Club*, for February, contains the following articles: De Vries, "On Atavistic Variation in *Œnothera cruciata*"; Clements, "Nova Ascomycetum genera speciesque"; Peck, "New Species of Fungi"; Hollick, "A Fossil Petal and a Fossil Fruit from the Cretaceous (Dakota Group) of Kansas"; Rowlee, "Notes on Antillean Pines with description of a New Species from the Isle of Pines"; and Murrill, "Polyporaceæ of North America, II, The Genus Polyporus."

Torreya, for February, contains the following articles: Underwood, "Notes on Southern Ferns, I"; Seymour, "Trichomanes petersii Found Anew"; Harper, "A Unique Climbing Plant"; Britton, "An undescribed Eleocharis from Pennsylvania"; and Earle, "Key to the North American Species of Stropharia."

Torreya, for March, contains Parish, "Vital Persistency of Agave Americana"; Earle, "Key to the North American Species of Lentinus, I"; Ramaley, "Pubescence of Species of Astragalus"; Cockerell, "Insect Visitors of Scrophularia"; and Haynes, "Some interesting Hepaticæ from Maine."

Vol. II of the *Memoirs of the New York Botanical Garden*, issued January 20, consists of a treatise by Professor MacDougal on the "Influence of Light and Darkness upon Growth and Development."

Minnesota Botanical Studies, 3d Series, Part 1, issued March 21, 1903, contains the following papers: Ramaley, "Observations on Egregia menziesii"; Butters, "Observations on Trichoglœa lubrica";

Holtz, "Observations on Pelvetia"; Hone, "Petalonema alatum in Minn."; N. B. P. Nelson, "Observations upon some Algæ which cause 'Water Bloom'"; Hillesheim, "Some Observations on the Staining of the Nuclei of Fresh-water Algæ"; Crosby, "Observations on Dictyosphæria"; Brand, Stapfia cylindrica in Minn."; Powell, "Observations on some Calcareous Pebbles"; "Lilley, Nitella batrachosperma in Minn."; and Wheeler, "Catalog of Minnesota Grasses."

The *Bulletin of the Southern California Academy of Sciences*, of February 1, contains the following botanical articles: Hasse, "Contributions to the Lichen-flora of the California Coast Islands"; Parish, "Two New Plants from Southern California"; and Davidson, "New Records for Los Angeles County."

Professors Aven Nelson and Cockerell have described several new plants from New Mexico in recent leaflets of the *Proceedings of the Biological Society of Washington*, which also contain a revision of Psilostrophe by the first-named author.

Bailey's Queensland Flora has reached Part VI,— Alismaceæ to Filices,— which concludes the work, making a volume of 2015 pages, in addition to separately paged prefatory matter. It is illustrated by 88 plates.

No. 8 of Koorder's and Valeton's Additamenta ad Cognitionem Floræ Arboreæ Javanicæ, issued as *Mededeelingen uit 's Lands Plantentuin*, No. LIX, deals with Rubiaceæ and Oleaceæ.

An illustrated article on "Saving the Southern Forests," by Price, is published in *The World's Work* for March.

F. L. Sargent has published— Cambridge, 1903 — a useful little "Key to Common Deciduous Trees in Winter and Key to Common Woods."

Illustrated accounts of Sisal or henequen fiber, as produced in Yucatan, are given in *Advance Sheets of Consular Reports No. 1582*, the *National Geographic Magazine* for April, and *The American Inventor* for May 1, all by Consul E. H. Thompson, of Progress.

Further studies on the Root-tubercles of Leguminosæ and their causation are published by Hiltner and Störmer, as Heft 3 of the third volume of *Arbeiten aus der Biologischen Abtheilung für Land- und Forst-Wirthschaft am Kaiserlichen Gesundheitsamte.*

The John Crerar Library, of Chicago, has issued a list of bibliographies of special subjects, among which botany finds place.

The *Botanical Gazette* for November contains the following papers: Johnson, "On the Development of Certain Piperaceæ"; Kraemer, "The structure of the Starch Grain"; Aven Nelson, "Contributions from the Rocky Mountain Herbarium, IV"; and Evans, "A New Hepatic from the Eastern United States."

Broteria, Revista de sciencias naturæs do Collegio de S. Fiel, is the title of a new annual, issued at Lisbon. The frontispiece of the first volume is a picture of the statue of the botanist Broteri, in the botanic garden at Coimbra, accompanied by a short account of his life and work.

The *Journal of Mycology*, for December, contains the following articles: Morgan, "A New Genus of Fungi [Sporocystis]"; Sanders, "Interesting variations in the appendages of Podosphæra oxyacanthæ"; Holway, "Notes on Uredineæ, I"; Schaffner, "Ohio Stations for Myriostoma"; Ellis and Bartholomew, "New Species of Fungi from Various Localities": Morgan, "The Discomycetes of the Miami Valley, Ohio"; Kellerman, "Notes from Mycological Literature, III"; Kellerman, "Index to North American Mycology, continued."

Meehan's Monthly, which has regularly included a plate with commentary dealing with native plants, in each number, stopped with the December number but is serially continued by a new journal, *Floral Life*.

Part 26 of *Pittonia*, the opening number of the fifth volume, consists of a series of papers by Professor Greene, dealing with a considerable number of genera of phanerogams.

The Plant World for October contains the following articles: Safford, "Extracts from the Note Book of a Naturalist on the Island of Guam, II"; Fitzpatrick, "A Study of the Island Flora of the Mississippi River near Sabula, Iowa"; Niles, "Origin of Plant Names, II, the Lady's Slippers and Moccasin Flowers"; Barrett, "The West Indian Corkwood"; and Bates, "The Disputed Longevity of Certain Plants."

Rhodora for November contains the following articles: Evans, "Notes on New England Hepaticæ"; Fernald, "Variations in Glaux in America"; Jones, "Pogonia affinis in Vermont"; Holt, "Is Cirsium palustre a Native of New Hampshire?" Morrell, "Lamium album in Maine"; Fernald, "Lists of New England plants, X, Carex"; and Beal, "Seed Throwing of Viola."

Torreya for November contains the following articles: Cannon,

"Field Notes on Rhododendron catawbiense"; Earle, "Key to the North American Species of Cortinarius, I"; Underwood, "Two New Species of Selaginella in the Southern Flora"; Lloyd, "Vacation Observations, I"; Howe, "Note on the Report of the Brown-Harvard Expedition to Nachvak, Labrador"; and Hazen, "The Habitat of the Slender Cliff Brake."

The *Bulletin of the Torrey Botanical Club* for November contains the following articles: Underwood, "American Ferns, IV, the Genus Gymnogramme of the Synopsis Filicum"; Knowlton, "Notes on the Fossil Fruits and Lignites of Brandon, Vt."; Piper, "New and Noteworthy northwestern Plants"; and Salmon, Supplementary Notes on the Erysiphaceæ."

Volume X of the *Memoirs of the Torrey Botanical Club*, issued in November, is devoted to a history of pre-Clusian botany in its relation to Aster, by Burgess.

In *University Studies* (of the University of Nebraska) for December, Dr. Clements analyzes the use of Greek and Latin in biological nomenclature, lays down a series of rules, and gives a very large number of correctly formed generic names which he proposes to substitute for a like number of incorrectly formed names now in use.

The proper terminology of groups, in botany, is the subject of a short but incisive note by Professor Underwood in *Science* of November 28.

A flora of the West Indian island of St. Croix, by Millspaugh, is printed as No. 7 of the current volume of botanical *Publications of the Field Columbian Museum.*

In the *Nuovo Giornale Botanico Italiano* for October, is concluded a critical study of the Italian species of Atriplex.

No. 17 of Dr. Holm's Studies in the Cyperaceæ, in the *American Journal of Science* for December, deals with segregates of Carex tolmiei.

Curtis's Botanical Magazine for November contains a figure of a curious aquatic Amaryllid, Crinum natans, of Africa.

Out West, for December, contains an illustrated article on *Pinus torreyana*, by Helen L. Jones.

A paper by Minnie Reed, on "Two New Ascomycetous Fungi Parasitic on Marine Algæ," is issued under date of November 20, as a brochure of the first botanical volume of the *University of California*

Publications. Both are referred to the genus Guignardia, and considered to be undescribed, as is also the species of Prasiola on which one of them occurs.

An account of larch and spruce fir canker, and the fungi involved, by Massee, is reprinted from the *Journal of the Board of Agriculture* of London, for September.

Fascicle 2 of Sydow's Monographia uredinearum carries the number of species of Puccinia up to 595.

An account of tea, its cultivation and preparation for the market, by Williamson, is contained in part 4 of the fourth volume of *Transactions of the Edinburg Field Naturalists' and Microscopical Society*.

A study of the species of Eucalyptus cultivated in the United States, by McClatchie, forming a large and well illustrated paper, is published as *Bulletin no. 35* of the Bureau of Forestry of the Department of Agriculture.

A practical little hand-book for the forester, dealing with measurements of standing and cut timber and the like, is published by H. S. Graves as *Bulletin no. 36* of the Bureau of Forestry of the Department of Agriculture.

An account of wild rice, Zizania aquatica, and its use by the Indians, is published by A. E. Jenks in part 2 of the 19th *Annual Report of the Bureau of American Ethnology*, and is illustrated by numerous plates.

No. 437 was mailed May 26, 1903.